

FINAL REPORT

Odontocete Cetaceans: Quantifying Behavioral Ecology and Response to Predators Using a Multi-Species Approach

SERDP Project RC-2154

MARCH 2016

Dr. Andrew J. Read
Duke University

Distribution Statement A

This document has been cleared for public release



This report was prepared under contract to the Department of Defense Strategic Environmental Research and Development Program (SERDP). The publication of this report does not indicate endorsement by the Department of Defense, nor should the contents be construed as reflecting the official policy or position of the Department of Defense. Reference herein to any specific commercial product, process, or service by trade name, trademark, manufacturer, or otherwise, does not necessarily constitute or imply its endorsement, recommendation, or favoring by the Department of Defense.

REPORT DOCUMENTATION PAGE				Form Approved OMB No. 0704-0188	
Public reporting burden for this collection of information is estimated to average 1 hour per response, including the time for reviewing instructions, searching existing data sources, gathering and maintaining the data needed, and completing and reviewing this collection of information. Send comments regarding this burden estimate or any other aspect of this collection of information, including suggestions for reducing this burden to Department of Defense, Washington Headquarters Services, Directorate for Information Operations and Reports (0704-0188), 1215 Jefferson Davis Highway, Suite 1204, Arlington, VA 22202-4302. Respondents should be aware that notwithstanding any other provision of law, no person shall be subject to any penalty for failing to comply with a collection of information if it does not display a currently valid OMB control number. PLEASE DO NOT RETURN YOUR FORM TO THE ABOVE ADDRESS.					
1. REPORT DATE (DD-MM-YYYY) 21-03-2016		2. REPORT TYPE Final		3. DATES COVERED (From - To) Jul 2011 - Mar 2016	
4. TITLE AND SUBTITLE Odontocete Cetaceans: Quantifying Behavioral Ecology And Response to Predators using a Multi-Species Approach				5a. CONTRACT NUMBER RC-2154	
				5b. GRANT NUMBER	
				5c. PROGRAM ELEMENT NUMBER	
6. AUTHOR(S) Read, Andrew J. Southall, Brandon, E. Nowacek, Doug P. Friedlaender, Ari S.				5d. PROJECT NUMBER	
				5e. TASK NUMBER	
				5f. WORK UNIT NUMBER	
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) Duke University Southall Environmental Assoc. Woods Hole Oceanograph. Inst. Oregon State University				8. PERFORMING ORGANIZATION REPORT NUMBER	
9. SPONSORING / MONITORING AGENCY NAME(S) AND ADDRESS(ES) Strategic Environmental Research & Development Program Arlington, VA 22350				10. SPONSOR/MONITOR'S ACRONYM(S) SERDP	
				11. SPONSOR/MONITOR'S REPORT NUMBER(S) RC-2154	
12. DISTRIBUTION / AVAILABILITY STATEMENT Unlimited					
13. SUPPLEMENTARY NOTES					
14. ABSTRACT The primary objective of this project was to improve knowledge of the baseline behavioral ecology of odontocete cetaceans and, specifically, understanding of how these animals respond to certain types of sound. Playback experiments were conducted to determine how short-finned pilot whales (<i>Globicephala macrorhynchus</i>) and Risso's dolphins (<i>Grampus griseus</i>) respond to the sounds of mammal-eating killer whales (<i>Orcinus orca</i>), some of which have similarities to certain military sonars. A secondary objective of the project was to increase understanding of the baseline behavior of odontocete cetaceans and, in particular, to understand some of the drivers of variation observed in this baseline. This portion of the work focused on short-finned pilot whales, which exhibit considerable variation in their foraging behavior. Nevertheless, they are one of the most tractable study species of pelagic odontocetes.					
15. SUBJECT TERMS Cetaceans, Behavioral Response, Social Behavior, Playback Experiments, Predator, Sonar, Mitigation					
16. SECURITY CLASSIFICATION OF: U			17. LIMITATION OF ABSTRACT UU	18. NUMBER OF PAGES 84	19a. NAME OF RESPONSIBLE PERSON Andrew J. Read
a. REPORT U	b. ABSTRACT U	c. THIS PAGE U			19b. TELEPHONE NUMBER (include area code) 252-504-7590

Table of Contents

Abstract.....	1
Objective	3
Background	5
Chapter 1: Initial Work.....	7
1.1 Field Tests of DTAG Attachments.....	7
1.2 Development of a Lightweight Broadband Underwater Sound Source	8
1.3 Development of Experimental Stimuli	11
Chapter 2: Short-finned pilot whales and Risso’s dolphins respond strongly and divergently to non-linear killer whale calls	13
2.1 Introduction	13
2.2 Materials and Methods	15
2.3 Results	23
2.4 Discussion.....	32
Chapter 3: A Multi-Scale Approach to Understanding Temporal Variation in the Foraging Patterns of Short-Finned Pilot Whales.....	35
3.1 Introduction	35
3.2 Materials and Methods	36
3.3 Results	39
3.4 Discussion.....	44
Chapter 4: Hidden Markov Models reveal complexity in the diving behavior of short-finned pilot whales	47
4.1 Introduction	47
4.2 Materials and Methods	48
4.3 Results	51
4.4 Discussion.....	57
Chapter 5: Conclusions and Implications for Future Research/Implementation	61
5.1 Is the Response of Odontocetes to Potential Threats Mediated by Patterns of Social Organization?.....	61
5.2 Biological functions of the monophonic and biphonic killer whale calls relative to killer whale social behavior and predator-prey dynamics.....	64
5.3 Research Gaps Related to Acoustic Ecology.....	65
5.4 Similarities between killer whale signals and MFAS sound profiles	66
Literature Cited	70
Appendices.....	84

List of Tables

Table 1.1 Summary of Version 3.2 DTAG deployments on small odontocetes in the SOCAL-BRS field study during 2012.....	8
Table 2.1. Maximum RMS (dB re: 1uPa) broadband received levels (Max RL)for all playbacks. X denotes playback exemplars that were not detected on the tag acoustic record. An asterisk denotes that the DTAG jettisoned before the call was played.....	23
Table 2.2. Playback calls, stimulus order, and group context for each pilot whale playback trial.	24
Table 2.3. Playback calls, stimulus order, and group context for each Risso’s dolphin playback trial.....	25
Table 2.4. Distance between focal pilot whale and sound source during playback trials. Red indicates a significant change in heading, as determined using a two-sample circular t-test on the heading data collected on the DTAG for two minutes before and after each playback.	31
Table 2.5. Distance between focal Risso’s dolphin and sound source during playback trials. Red indicates a significant change in heading, as determined using a two-sample circular t-test on the heading data collected on the DTAG for the two minutes before and after each playback.....	31
Table 3.1. Deployments of SLTDRs on short-finned pilot whales off Cape Hatteras, North Carolina.....	37
Table 3.2. Confusion matrix for Random Forest Analysis	40
Table 3.3. Confusion matrix for Conditional Inference Tree	40
Table 3.4. Comparison of overall accuracy and statistics between the two classification methods	40
Table 3.5. Variable importance determined in Random Forest Analysis. The mean decrease accuracy reflects the reduction in accuracy if the variable was removed from a decision tree.....	41
Table 3.6 Foraging bout analysis	41
Table 3.7. Dive bout analysis.....	41
Table 3.8. Diel variation in foraging rates, dive rates, and average depths	44
Table 4.1. Summary of tagging information, including the number of dives assigned to each state. Tag ID is based on the Julian day with the letter representing the sequential order in which the animal was tagged (a= first animal tagged that day, b = second and so forth). Biopsy, Y is a biopsy obtained, N is no biopsy obtained. Sex was obtained from the biopsy data, M= male, F=female, U= unknown (sample not processed), - = no biopsy taken. Total dives indicates the number of dives used in the analysis. Number of dives per state shows the allocation of dives from the HMM.	50
Table 4.2. State summaries of observed variables for each state.....	51
Table 4.3. Transition probabilities for both states and number of dives within each state.....	55

List of Figures

Figure 1.1 A damaged DTAG recovered from a brief deployment on a bottlenose dolphin off Cape Hatteras, North Carolina.	7
Figure 1.2 Lightweight Broadband Underwater Sound Source deployed during field trials in 2012.....	9
Figure 1.3 Transmit voltage response for each of four elements prior to frequency compensation, showing differential resonance frequencies across the requested operating band (0.5-10 kHz).	9
Figure 1.4 0.1-20 kHz frequency sweep as requested from the control software (left), filtered and transmitted to the transducer elements (middle) and received at 1 m with a calibrated hydrophone (right).	10
Figure 1.5. Tonal calibration stimuli at 1 kHz (left) and 4 kHz (right) measured at 1m from the LUWBUSS. Requested source levels were 160 dB re 1 μ Pa-m. Measured source levels were 160.4 and 161.6 dB re 1 μ Pa-m for 1 and 4 kHz respectively.	10
Figure 1.6. Requested and transmitted spectrograms of an individual pilot whale stimulus...	11
Figure 1.7. Test stimuli calibration measurements at 1 m from the LUWBUSS. Requested source levels were 160 dB re: 1 μ Pa-m in both cases. Measured source levels were 158.1 and 156.1 dB re 1 μ Pa-m for these pilot whale and humpback whale exemplars.	12
Figure 1.8. Test stimuli measured at ~4 m from the LUWBUSS during playbacks on 12 May 2012. Requested source levels were 160 dB re: 1 μ Pa-m in both cases. Measured source levels were 152.9 and 156.1 dB re 1 μ Pa for these individual elements of killer whale and pilot whale exemplars.	12
Figure 2.1 Spectrograms of calls from mammal-eating killer whales used in playback experiment with short-finned pilot whales and Risso's dolphins *denotes that a strong response was observed during field trials.	18
Figure 2.2. Spectrograms of short-finned pilot whale calls from Tenerife used in playback experiment with short-finned pilot whales off Cape Hatteras.	19
Figure 2.3. Spectrograms of humpback social sounds from Stellwagen Bank used in playback experiment with short-finned pilot whales and Risso's dolphins.	20
Figure 2.4. Spectrograms of Risso's dolphin calls from southern California used in playback experiment with Risso's dolphins off Catalina Island.	21
Figure 2.5. Examples of a lack of reaction (left) and a strong reaction (right) of short-finned pilot whales to playbacks of monophonic and biphonic mammal-eating killer whale calls. The reactions included increased flow noise, ODBA and heading variance. Each panel displays a 30-second period before, during and after presentation of a killer whale call and provides values for: (A) transmitted and received signals; (B) spectrogram of the acoustic record; (C) flow noise, which is a proxy for the speed of the tagged animal; (D) depth profile of the tagged animal; (E) ODBA, which is a proxy for movement of the tagged animal; and (F) circular plots of heading of the tagged animal.....	25
Figure 2.6. Response of Risso's dolphin Gg13_228b to playback of a mammal-eating killer whale call. Similar to the response seen in pilot whales, we observed an increase in flow noise, ODBA and heading variance during presentation of the killer whale call. The figure displays the 30 seconds before, during and after the playback and displays: (A) spectrogram of the acoustic record; (B) flow noise, which is a proxy for the speed of the tagged animal; (C) depth profile of the tagged animal; (D) ODBA, which is a proxy for movement of the tagged animal; (E) pitch and fluke strokes by the tagged animal; and (F) heading of the tagged animal.	26

Figure 2.7. Parameter estimates, together with with 95% confidence intervals (CI) of Gaussian GEE for ODBA for before, during and after playbacks of various exemplars to short-finned pilot whales. Horizontal lines represent parameter estimates and vertical lines represent the 95% CI derived from parametric bootstrap of the fit parameters of the GEE. ODBA levels during the playback of biphonic mammal-eating killer whale calls (highlighted in yellow) were significantly higher than baseline levels. No other period (before, during or after) for any other stimulus were found to be significantly different from baseline levels.	27
Figure 2.8. Parameter estimates of Poisson GEE of pilot whale call counts before and after playbacks of each stimulus type. Horizontal lines represent parameter estimates and vertical lines represent the 95% CI derived from parametric bootstrap of the fit parameters of the GEE. Call counts following the playback of biphonic mammal-eating killer whale calls (highlighted in yellow) were significantly higher than baseline or before levels.	28
Figure 2.9. Boxplots of ODBA values for 30-second time bins (before, during and after) for three playback stimuli for each tagged pilot whale. Highlighted in yellow are the playbacks of biphonic killer whale calls and in green is the single monophonic call (Oo-10) that elicited a response. All five animals exhibited an increase in ODBA during the playback followed by a reduction in ODBA.....	29
Figure 2.10. Boxplots of ODBA values for 30-second time bins (before, during and after) for three playback stimuli for each tagged Risso's dolphin. Highlighted in yellow is the playback of a biphonic killer whale call and in green is the single monophonic call (OoO-10) that elicited a response. Risso's dolphins displayed a similar response to pilot whales, which included an increase in ODBA during the playback followed by a reduction in ODBA.	30
Figure 2.11. Circular plots of heading relative to the sound source for 30 seconds before and after playbacks of killer whale exemplar Oo-10 to a pilot whale (left) and a Risso's dolphin (right). Bearing of the sound source to the focal animal was determined using known location of the sound source and the estimated heading of the focal animal as reconstructed from the focal follow points.	32
Figure 3.1. Tagging locations for DTAGs and SLTDRs on short-finned pilot whales off Cape Hatteras, North Carolina.	37
Figure 3.2. Images of LIMPET and DTAGs deployed on pilot whales GmTag087 and Gm12_161a off Cape Hatteras, North Carolina.	38
Figure 3.3. Results of DTAG analysis. The pane at left is a plot of maximum depth vs. duration with red circles representing non-foraging dives and black circles representing foraging dives. The pane at right is a classification tree produced by analysis of predictors of foraging dives. Bar plots in the non-branching nodes indicate the relative dropouts with particular combinations of relative predictors.	40
Figure 3.4. Surface durations following foraging bouts. The black dashed line represents a breakpoint in bout durations (4.53 hours). The red dashed line represents minimum surface duration following the break (1.01 hours).....	42
Figure 3.5. Surface durations following dive bouts.....	42
Figure 3.6. Dive record of pilot whale GmTag085 with bouts highlighted by shading	43
Figure 3.7. Bout durations for each SLTDR deployment.....	43
Figure 3.8. Box and whisker plot of depth of foraging dives during day and night.	44
Figure 4.1. Dive allocation per state for all dives from all individuals. Red = state 1, blue = state 2, green = state 3, purple = state 4. Top panel shows all dives from all states. Bottom four panels show each state individually. Note different x and y axis scale.	53

Figure 4.2. State allocation per dive for each of the three observed variables. Red represents state 1; blue represents state 2; green represents state 3 and purple represents state 4....	54
Figure 4.3. Range overlap (min-max) for each of the three variables for all four states.	54
Figure 4.4. Dive allocation per individual. Red = state 1, blue = state 2, green = state 3, purple = state 4. See Table 4.1 for individual information; First column, individuals 143a-151b; second column, individuals 185b-208a; third column, individuals 209a-149b; fourth column, individuals 150b-280a Note different x and y axis scales.	55
Figure 4.5. Dive profile data from three individual pilot whales (top: Gm10_187b, middle: Gm10_266a, bottom: Gm10_267a) with the probability of state mapped onto the dives. Red lines indicate highest probability of being in state 1, blue lines indicate highest probability of being in state 2, green lines indicates highest probability of being in state 3 and purple lines highest probability of being in state 4. Grey lines indicate data not used in the analysis, this includes information classified as at the surface, incomplete dives or dives lacking acoustic records. Black asterisks identify individual buzzes, yellow moon on x axis indicates approximate time of sunset (20:00) and yellow sun indicates approximate time of sunrise (6:00). Note different x and y axis ranges.....	56
Figure 5.1. Spectrograms of biphonic calls from a mammal-eating killer whale from the LWBBUSS (top) and received on a DTAG on a short-finned pilot whale off Cape Hatteras (below).	67
Figure 5.2. Simulated MFAS signal recorded at the source (A) and on a DTAG deployed on a blue whale off southern California (B).	68
Figure 5.3. Two-element MFAS signal from a 53C surface vessel (top) and two pings from a helicopter dipping sonar (bottom), both recorded off southern California.	68

List of Acronyms

ANOM	Analysis of Means
ANOVA	Analysis of Variance
ANSI	American National Standards Institute
APS	Applied Physical Sciences Corporation
BRS	Behavioral Response Study
CEE	Controlled Exposure Experiments
DCS	Decompression Sickness
DTAG	Digital Acoustic Tag
GPS	Global Positioning System
LUWBUSS	Lightweight Broadband Underwater Sound Source
MD	Mahalanobis Distance
MFAS	Mid-Frequency Active Sonar
MOCHA	Multi Study Ocean Acoustics Human Effects Analysis
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
ODBA	Overall Dynamic Body Acceleration
RHIB	Rigid-Hulled Inflatable
RL	Received Level
RMS	Residual Mean Squares
SPL	Sound Pressure Level
SNR	Signal-to-Noise Ratio
VHF	Very High Frequency

Keywords

Cetaceans, Behavioral Response, Social Behavior, Playback Experiments, Predator, Sonar, Mitigation.

Acknowledgements

We thank our field crews for tagging and tracking pilot whales and Risso's dolphins off Cape Hatteras and in Southern California. In particular, we appreciate the hard work of our core field crew who worked on both coasts, including: Matt Bowers, John Calambokidis, Heather Foley, Zach Swaim, and Danielle Waples. The captain and crews of the NOAA vessel *SRVX*, the FV *Hog Wild* and the MV *Truth* ensured that we were both safe and productive at sea. Recordings of pilot whales, killer whales and humpback whales were generously provided by Frants Jensen, Volker Deecke, Sofie Van Parjs and Danielle Cholewiak; Lynne Williams undertook the time consuming job of creating the experimental stimuli from these recordings. We thank Alex Bocconcelli, Tom Hurst and Dan Bogorff from the Woods Hole Oceanographic Institution for assistance with DTags. We appreciate the assistance of scientists involved in the SOCAL-BRS experiment for their assistance with field tests of Version 3 DTags. Vincent Janik, Frants Jensen, Laela Sayigh, Volker Deecke and Stacy DeRuiter helped to design our experimental protocol at the March 2012 workshop. Jennifer Dunn organized the workshop and provided administrative oversight of this grant. Matt Bowers and Nicola Quick conducted most of the analysis presented here and we thank Stacy DeRuiter, Catriona Harris and Len Thomas for their invaluable assistance with this portion of the work. Field research on short-finned pilot whales off Cape Hatteras was conducted under: NOAA Permit 1421-03, issued to Peter Tyack; NOAA Permit 779-1633, issued to Keith Mullin; and NOAA General Authorization 16185, issued to Andrew Read and approved by the Institutional Animal Use and Care Committee of Duke University. Field research on Risso's dolphins was conducted under NMFS Permit 14534, issued to NMFS Office of Science and Technology; PI: Brandon Southall. We thank SERDP for funding this project and the Scientific Advisory Board for their support and suggestions. Finally, we thank Dr. John Hall, the Program Manager for Resource Conservation and Climate Change, and his staff, for all their assistance and for making sure that our project was a success.

Abstract

Objectives

The primary objective of this project was to improve knowledge of the baseline behavioral ecology of odontocete cetaceans and, specifically, understanding of how these animals respond to certain types of sound. A secondary objective of the project was to increase understanding of the baseline behavior of odontocete cetaceans and, in particular, to understand some of the drivers of variation observed in this baseline. This portion of the work focused on short-finned pilot whales (*Globicephala macrorhynchus*), which exhibit considerable variation in their foraging behavior. Nevertheless, they are one of the most tractable study species of pelagic odontocetes.

Technical Approach

Playback experiments were conducted to determine how short-finned pilot whales and Risso's dolphins (*Grampus griseus*) respond to the sounds of mammal-eating killer whales (*Orcinus orca*), some of which have similarities to certain military sonars. Specifically, this work addressed whether social structure influences the response to the sounds of these predators by comparing the behavioral responses of the two species, which exhibit contrasting patterns of social organization.

The baseline foraging and diving behavior of short-finned pilot whales also were described using two types of tag records. First, data streams were combined from short-term Digital Acoustic Tags (DTAGs) with long-term Satellite-Linked Time Depth Recorders (SLTDRs) to analyze long-term foraging patterns, evaluate diurnal variation in foraging behavior, and determine pattern and variation in foraging bouts. Second, multi-state hidden Markov models were used to classify short-finned pilot whale diving behavior using DTAG data. This approach enabled classifying dives objectively into behavioral states and to objectively determine transitions between states.

Results

Short-finned pilot whales and Risso's dolphins reacted strongly and divergently to biphonic calls of mammal-eating killer whales, but not to most other call types. Following exposure to biphonic calls, focal groups of both species demonstrated increased cohesion, but exhibited different vocal and movement responses. Pilot whales increased their call rate and approached the sound source, but Risso's dolphins exhibited no change in their vocal behavior and moved in a rapid, directed manner away from the source. Thus, at least to a subset of mammal-eating killer whale calls, the two study species reacted in a manner that is consistent with their patterns of social organization. Pilot whales, which live in relatively permanent groups bound by strong social bonds, responded in a manner that built on their high levels of social cohesion. In contrast, Risso's dolphins exhibited an exaggerated flight response and moved rapidly away from the sound source.

Short-finned pilot whales off Cape Hatteras demonstrated considerable variation in their baseline diving and foraging behavior. The whales dove to depths of more than 1200 meters and for periods lasting for up to 26 minutes. Mean duration of a foraging bout was 2.18

hours, with an average of 6.1 dives per bout. Foraging bouts longer than 4.5 hours required at least an hour of recovery time at the surface. No discernable pattern emerged in surface durations following dive bouts. Surprisingly, no diel pattern was observed in foraging depth or duration. The hidden Markov model analysis demonstrated that the diving behavior of short-finned pilot whales is much more complex than a simple dichotomy of deep and shallow diving states. Four separate diving states were identified that showed patterns of state persistence and switching among states. Predictions of state were based on the distribution of three readily observed variables: dive duration, maximum depth and number of foraging buzzes. Taken together, these baseline observations suggested that short-finned pilot whales are able to adapt their diving strategy on a dive by dive basis, switch effectively between different diving states, and do so while maintaining foraging efficiency and social cohesion.

Benefits

The playback experiments described here facilitated identification of some of the key contextual factors of the behavioral responses to a threatening sound in two species of odontocetes. Short-finned pilot whales and Risso's dolphins reacted to biphonic calls of mammal-eating killer whales in a manner that is consistent with our knowledge of their social organization. Furthermore, these biphonic calls share several characteristics with mid-frequency active sonars (MFAS). If odontocetes perceive the sounds of MFAS and the sounds of predators in a similar manner, or even if they merely respond to the two sound types in the same way, we can infer much about the nature and likely magnitude of the potential risks of MFAS by understanding the anti-predator response of each species. An important conclusion resulting from this study is that there is considerable merit from pursuing this line of reasoning: that is, constructing a formal conceptual model of the response of odontocetes to potential threats and using interacting factors such as habitat, social structure, and body size as predictors of response. A matrix of these predictive factors can be used to predict the behavioral response of odontocetes to any threat, including MFAS, at least in a coarse manner.

In addition, the project's work on the diving and foraging behavior of short-finned pilot whales has generated an important baseline for future studies of disturbance with this species. The characterization of baseline diving and foraging behavior will benefit future behavioral response and playback studies, because one can now predict the probability that an animal will stop foraging, or switch from one diving state to another, under baseline conditions. This baseline information can then be used to predict the likelihood that a change will occur following exposure to a particular stimulus. Short-finned pilot whales do exhibit a considerable degree of inter- and intra-individual variation in their diving and foraging behavior, but this study was able to capture and describe important sources of this variation in its analysis.

Objective

The overall objective of our project was to improve our knowledge of the baseline behavioral ecology of odontocete cetaceans and, specifically, our understanding of how these animals respond to certain types of sound. We conducted our research in response to the SERDP Statement of Need (SON) Number SISON-11-02, *Behavioral Ecology of Cetaceans*. Our research addressed the first research need identified in the SON: *Quantify and model the baseline behavioral ecology of key cetacean species and taxonomic groups to include foraging, reproduction, predator avoidance and social behaviors and associated environmental and habitat conditions*.

To achieve this objective, we conducted playback experiments to determine how odontocete cetaceans respond to the sounds of mammal-eating killer whales, some of which have similarities to certain military sonars (see below). Specifically, we investigated whether social structure influences the response to acoustic stimuli by examining the behavioral responses of two odontocete species, short-finned pilot whales (*Globicephala macrorhynchus*) and Risso's dolphins (*Grampus griseus*), with contrasting patterns of social organization, to the sounds of these predators. We focused our work on these mid-size odontocete cetaceans because they and other similar species comprise a large proportion of the regulatory takes requested by the U.S. Navy for incidental harassment of marine mammals during training exercises, but for which empirical data on responses to sound exposure are almost entirely lacking.

Our two focal species exhibit different patterns of social organization. Short-finned pilot live in permanent family groups from which female offspring do not disperse. Such behavior is extremely rare in mammals and requires that breeding occur between individuals from different groups (Connor 2000). Short-finned pilot whales are also one of a small number of mammalian species (including humans and killer whales) in which females exhibit reproductive senescence (Kasuya and Marsh 1984).

In contrast, the social structure of Risso's dolphins has been described as 'stratified social organization,' in which adult males and adult females and their calves form relatively stable, but separate, pods (Hartman et al. 2008). Association patterns vary among age classes, but are most stable in adult males and most fluid in sub-adults. Furthermore, groups of Risso's dolphins exhibit relatively low levels of relatedness (Gaspari 2004). Thus, the relatively open pattern of social organization of this species differs significantly from the permanent family groupings exhibited by pilot whales.

We used these differences in the social behavior of the two species to generate predictions of their response to the sounds of predators. We predicted that groups of pilot whales would increase their social cohesion in the perceived presence of predators to afford greater protection to related family members. In contrast, we predicted that Risso's dolphins would show less social cohesion in the presence of predators and would be more likely to move away from the source of the sound. To achieve our objective, we conducted field playback experiments with short-finned pilot whales off Cape Hatteras, North Carolina and Risso's dolphins off southern California, using the calls of mammal-eating killer whales as the primary experimental stimulus.

A secondary objective of our project was to increase our understanding of the baseline behavior of odontocete cetaceans and, particularly, to understand some of the drivers of

variation observed in this baseline. We focused this portion of our work on short-finned pilot whales, which exhibit considerable variation in their foraging behavior, because they are one of the most tractable study species of pelagic odontocetes. The considerable degree of variation in the foraging behavior of this species hampers our ability to understand their response to a variety of stimuli, so we set about to better understand some of its ecological and behavioral drivers using tagging studies conducted at two different time scales.

Background

Exposure to tactical, mid-frequency active military sonars (MFAS) can have adverse effects on some species of odontocete cetaceans under certain environmental conditions. Some beaked whales appeared to be particularly sensitive to such sounds (Cox et al. 2006; D'Amico et al. 2009). Necropsy reports from stranded beaked whales indicated trauma similar to decompression sickness (Fernández et al. 2005), leading to hypotheses that an aversive behavioral response to MFAS could lead to DCS in some cetaceans (Cox et al. 2006). It remains unclear, however, why some odontocete species react so strongly to these tactical sonars or under what conditions such extreme responses occurred.

Interestingly, however, there are suggestions that beaked whales and perhaps other odontocetes respond to tactical sonar in a manner that is consistent with their response to predators. Zimmer and Tyack (2007) first noted similarities between the acoustic signals used in tactical, mid-frequency military sonars and the social sounds made by mammal-eating killer whales (*Orcinus orca*). This led to a hypothesis (Tyack 2009a; Tyack et al. 2011) that the strong aversive responses exhibited by beaked whales might reflect an anti-predatory behavior, because the animals perceived sonar signals as the sounds of killer whales. Under certain conditions, therefore, a behavioral response to the perceived presence of predators could lead to physiological risk to individual beaked whales.

Tyack's hypothesis stemmed, in part, from the results of a behavioral response study (BRS) conducted in the Bahamas in 2007 and 2008. In this experiment, Blainville's beaked whales (*Mesoplodon densirostris*) were exposed to simulated MFAS and responded by changing their vocal and diving behavior and steadily moving away from the source. The beaked whales responded in a similar fashion to the sounds of mammal-eating killer whales, although their response to the predator calls was more pronounced than to that of the simulated MFAS (Tyack et al. 2011). In contrast, short-finned pilot whales, which live in permanent family groups, responded to the sounds of mammal-eating killer whales with a suite of social alerting and defensive responses, including an elevated vocalization rate and increased social cohesion (Tyack 2009a).

We designed our work to build on these early observations and to gain further insight into the nature of this anti-predator response and the contextual factors that drive it. In particular, we were interested in whether the social structure of a species would affect its response to the sounds of predators or the occurrence of MFAS. Initially we proposed conducting playback experiments with a variety of odontocete species with different patterns of social structure, but due to logistical constraints (see section on *Initial Work* below), we concentrated our work on two species with contrasting patterns of sociality.

In our experimental work we used a suite of methods commonly employed in behavioral response studies, in which the response of a focal animal is observed before, during, and after exposure to a particular sound (Tyack 2009b; Southall et al. 2012). In this approach, a focal animal is equipped with a short-term recording device, such as a Digital Acoustic Tag (DTAG), to provide high-resolution data on potential kinematic and acoustic responses (Johnson and Tyack 2003; Johnson et al. 2009). In some field experiments, the amplitude of the sound is increased during the trial, so that a dose-response function can be generated. This was not the case for our experiments, in which we presented a focal animal and its social

group with brief, repeated calls from mammal-eating killer whales to simulate the distant presence of a predator.

Throughout our work we have benefitted from close collaboration with two other research groups conducting similar work: the SOCAL-BRS project (<http://sea-inc.net/socal-brs/>) and the 3-S project (<http://www.creem.st-and.ac.uk/mocha/open-meetings/brsworkshopsmmmlam>). Dr. Brandon Southall, the lead Principal Investigator on the SOCAL-BRS project (Southall et al. 2012) is also a co-Principal Investigator on our project and Dr. Ari Friedlaender is a co-Principal Investigator on both projects; we have benefitted greatly from the synergy of this collaboration. In addition, analysis of our results has been supported by colleagues from the Multi-Study Ocean Acoustics Human Effects Analysis (MOCHA) Project (<http://www.creem.st-and.ac.uk/mocha/>), funded by the Office of Naval Research, to develop and implement innovative methods for the analysis of cetacean behavioral response studies (Harris et al. 2016). We owe a great deal to the Principal Investigators and staff of these three projects, who have supported and facilitated our work.

Chapter 1: Initial Work

1.1 Field Tests of DTAG Attachments

During 2011 and 2012, we tested our ability to attach Digital Acoustic Tags (DTAGs) in field trials with several species of small odontocetes in the waters off Cape Hatteras, North Carolina and southern California. In May and June 2011, we attached 32 DTAGs to three species of odontocetes off Cape Hatteras: short finned pilot whales ($n = 15$); common dolphins *Delphinus delphis* ($n = 5$); and bottlenose dolphins *Tursiops truncatus* ($n = 12$). We employed both Version 2 and Version 3.1 DTAGs in these field trials. The median deployment time for the pilot whales (excluding four brief deployments) was 4.17 hours, meeting our experimental requirements of a deployment period of four hours. Unfortunately, our trials with the other two species were unsuccessful. In each case the dolphins responded to the attachment of the DTAG with a rapid corkscrew acceleration, shedding the tag immediately. In several trials, the DTAG was damaged during the brief period of attachment (Figure 1.1).



Figure 1.1 A damaged DTAG recovered from a brief deployment on a bottlenose dolphin off Cape Hatteras, North Carolina.

During the remainder of 2011 and into early 2012 we worked with engineers from the Woods Hole Oceanographic Institution to modify the attachment hardware of the Version 3 DTAG to make it more robust to these small delphinids. In July, August, and October 2012 we conducted field tests of the modified Version 3.2 DTAG in Southern California, taking advantage of the vessels and field team engaged in the SOCAL-BRS study. We deployed DTAGs on a single Risso's dolphin (*Grampus griseus*), five bottlenose dolphins and two common dolphins (Table 1.1). The deployment on the Risso's dolphin was successful, with a tag duration of almost four hours, consistent with previous tagging experiences with this species in SOCAL-BRS. The tag attachment attempts on bottlenose and common dolphins yielded short deployments, typically lasting a minute or less.

Thus, our experience with bottlenose and common dolphins off Southern California in 2012 was identical to our experience off Cape Hatteras in 2011. The improvements in the DTAG attachment system were not sufficient to keep the tags on these small, acrobatic dolphins for more than a minute or so. We concluded, therefore, that it would not be possible to attach the Version 3.2 DTAGs to common and bottlenose dolphins for periods sufficient to conduct acoustic playback experiments. This led to our decision to focus on short-finned pilot whales and Risso's dolphins for our playback experiments. The primary drawback to our revised experimental approach was that we were unable to examine the behavioral response of small-bodied, pelagic dolphins that live in large groups, such as common dolphins. We had hoped to include Cuvier's beaked whales (*Ziphius cavirostris*) as an experimental subject, but we never had the opportunity to conduct a playback with this species in either North Carolina or Southern California.

Table 1.1 Summary of Version 3.2 DTAG deployments on small odontocetes in the SOCAL-BRS field study during 2012.

Species	Date	Tag On	Tag Off	Tag Duration
Risso's Dolphin	27-Jul	14:14:05	18:04:00	3:49:55
Bottlenose Dolphin	28-Jul	13:15:00	13:16:00	0:01:00
Bottlenose Dolphin	3-Aug	9:15:00	9:16:00	0:01:00
Bottlenose Dolphin	3-Aug	10:30:00	10:31:00	0:01:00
Bottlenose Dolphin	3-Aug	10:45:00	10:46:00	0:01:00
Bottlenose Dolphin	3-Aug	11:00:00	11:01:00	0:01:00
Common Dolphin	19-Oct	10:05:00	10:06:00	0:01:00
Common Dolphin	19-Oct	10:07:00	10:08:00	0:01:00

1.2 Development of a Lightweight Broadband Underwater Sound Source

In our playback experiments, we used acoustic stimuli consisting of vocal signals recorded from three marine mammal species (described below) with sound energy across a relatively wide frequency range. We presented these stimuli to focal animals and their groups through a custom sound source built by Applied Physical Sciences Corporation (APS), using our design parameters. The objectives for this source were to be: (1) sufficiently lightweight to deploy by hand using a small davit arm; (2) powered independently of ship AC power; and (3) capable of transmitting a flat frequency response from 0.5-10 kHz.

The resulting Lightweight Broadband Underwater Sound Source (LWBBUSS) included four free-flooded ring transducers in a small housing, with a total weight of <20 kg, that was easily deployed by hand (Figure 1.1). To minimize extraneous electrical noise in the playback signals, the system was powered in the field by devoted 12V batteries and AC power was

supplied from a pure sine wave inverter (Magnum Energy MS2012). The requirement for flat response across such a broad frequency range resulted in a source design using four individual transducer elements (lightweight free-flooded rings), each with a resonant frequency response in different regions of the specified operating band (measured at the Navy's Dodge Pond test facility – see Figure 1.3).



Figure 1.2 Lightweight Broadband Underwater Sound Source deployed during field trials in 2012.

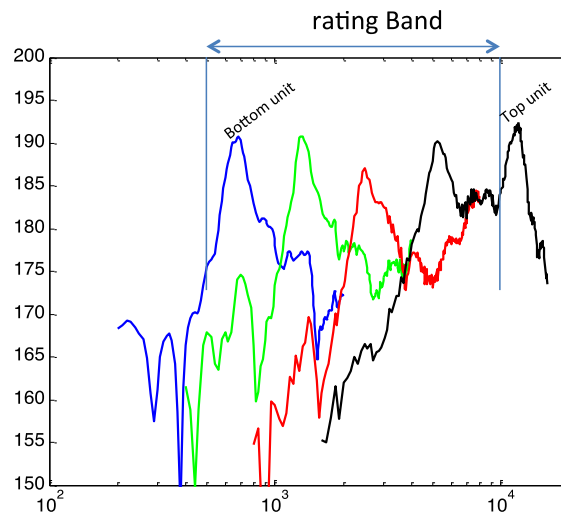


Figure 1.3 Transmit voltage response for each of four elements prior to frequency compensation, showing differential resonance frequencies across the requested operating band (0.5-10 kHz).

The LWBBUSS was controlled by a custom data acquisition board set and amplifier configuration designed and built by APS. Each of the transducer elements had a differential frequency response and a flat transmission across the 0.5-10 kHz band was required, so we used a virtual cross-element filtering network to generate signals sent to the amplifier for each transducer such that the effective output of the system was flat over the frequency band. The transmitted voltage frequency response calibration curves for the four transducers shown in Figure 1.3 were used to deliver appropriately frequency-weighted input signals to each

amplifier that retained the original signal phase. A band-pass filter (0.2-16 kHz) was applied to the input signal to provide some filtering of out-of-band noise. The result of this frequency compensation across the different transducer elements was that the transmitted spectrum of test signals (sent to the amplifier elements) was sufficiently controlled across all elements to ensure flat (± 2 dB) transmission across the operating band (Figure 1.4).

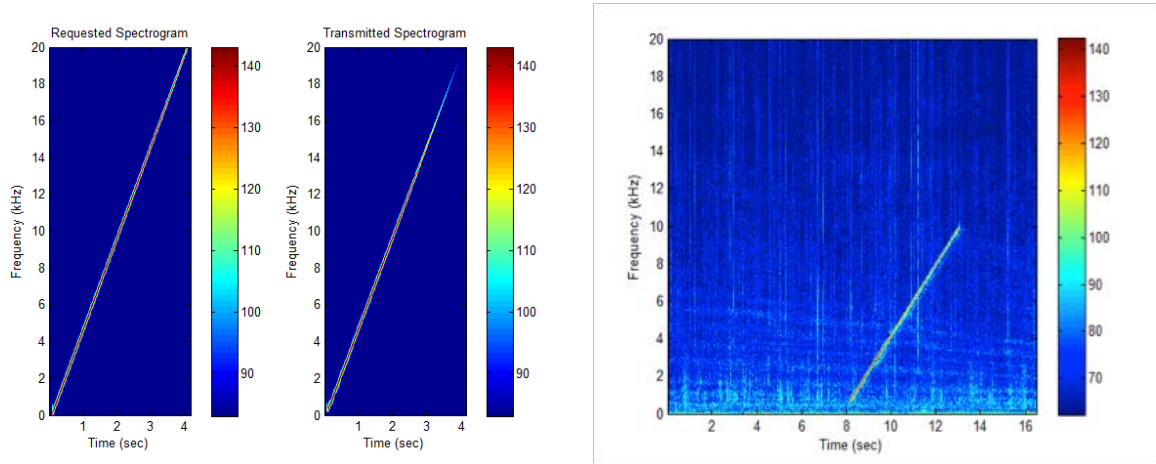


Figure 1.4 0.1-20 kHz frequency sweep as requested from the control software (left), filtered and transmitted to the transducer elements (middle) and received at 1 m with a calibrated hydrophone (right).

We confirmed output levels relative to requested and transmitted stimuli in the field by measuring calibration tones and test stimuli 1 m from the LWBBUSS. We measured transmitted tonal signals 1 m from the central axis of the LWBUSS with calibrated hydrophones (B&K 8103, HTI-96-min). Calibration measurements (in RMS dB re $1\mu\text{Pa}$ units of sound pressure level, hereafter dB SPL) were made with an oscilloscope (LeCroy Waverunner 6030A), MATLAB custom software and SpectraPlus (Pioneer Hill) measurement software. Results using tonal stimuli confirmed system performance within specifications described above for signals within the specified operating band (see examples in Figure 1.5).

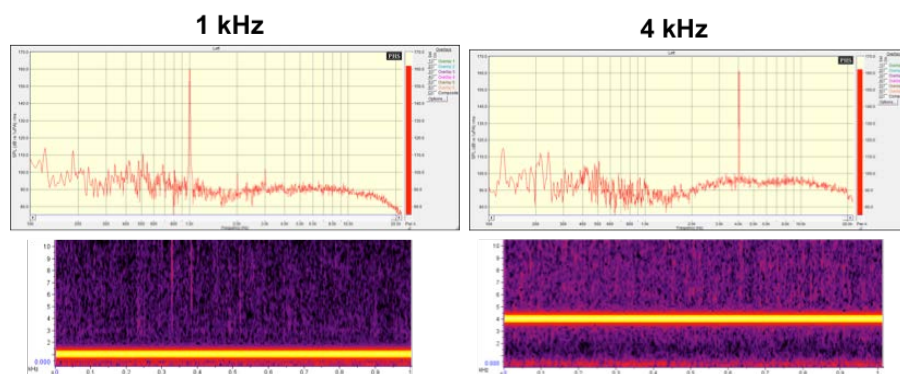


Figure 1.5. Tonal calibration stimuli at 1 kHz (left) and 4 kHz (right) measured at 1m from the LUWBUSS. Requested source levels were 160 dB re $1\mu\text{Pa}\cdot\text{m}$. Measured source levels were 160.4 and 161.6 dB re $1\mu\text{Pa}\cdot\text{m}$ for 1 and 4 kHz respectively.

1.3 Development of Experimental Stimuli

In March 2012 we invited a small group of participants to a workshop at Duke University to design the acoustic stimuli to be used in our field experiments. The workshop participants included experts on behavioral response studies, playback experiments, and the acoustic behavior of killer whales, pilot whales and other odontocetes.

The workshop participants agreed to a set of acoustic stimuli that were presented to each focal animal and its group. These stimuli consisted of three sets of signals: (1) mammal-eating killer whales recorded from DTAGs off the Pacific coast of the U.S. and Canada (the sound of potential predators); (2) pilot whale social sounds recorded using DTAGs in Tenerife, Spain (the sound of unfamiliar short-finned pilot whales) or Risso's dolphin social calls recorded using DTAGs in Southern California; and (3) humpback whale social sounds recorded with DTAGs from the Stellwagen Bank National Marine Sanctuary, off Cape Cod, Massachusetts (true controls). Killer whales occur regularly off the coast of North Carolina (Hairr 2012), but we are unaware of any recordings of these whales or, in fact, of any mammal-eating killer whales in the North Atlantic. Mammal-eating killer whales occur in the Bahamas, where they prey on a variety of odontocete species (Dunn and Claridge 2013). Other playback experiments in the North Atlantic have used recordings from the well-studied population of transient killer whales in the Pacific (Curé et al. 2012; Curé et al. 2013; Curé et al. 2015). We assumed that pilot whales off Cape Hatteras and Risso's dolphins off Southern California would recognize these sounds as those of a potential predator, even if the specific details of the calls were unfamiliar.

All stimuli were generated from high signal to noise recordings and normalized to have an equivalent maximum RMS voltage using a 200 ms RMS window. We used SpectraPlus and MATLAB tools to measure the relative broadband RMS levels of the signal and normalized using Adobe Audition to ensure output levels were balanced across all test stimuli. We then confirmed test signal levels again in SpectraPlus and MATLAB to ensure that relative output levels were within 1 dB across all test stimuli. Each stimulus was then transmitted through the LUWBUSS software to ensure that signals sent to the transducer elements retained signal integrity in both time and frequency domains (Figure 1.6) across the operating frequency band.

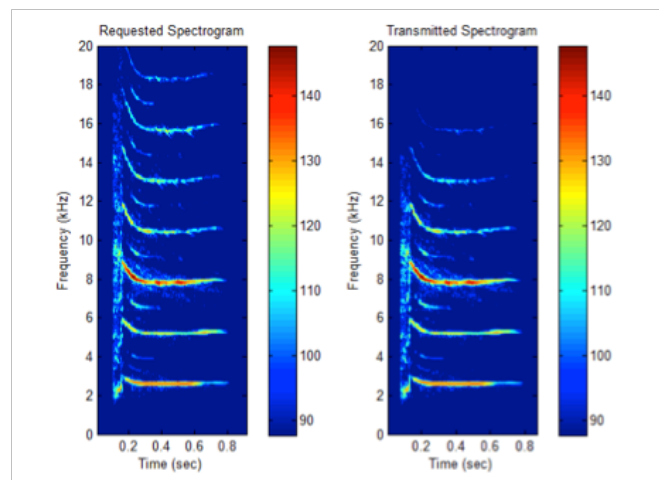


Figure 1.6. Requested and transmitted spectrograms of an individual pilot whale stimulus.

We calibrated test signals at 1 m from the source prior to playback experiments in areas far removed from experimental subjects (see two examples in **Figure 1.7**). Received broadband SPL levels for test stimuli of all three species were within ± 4 dB of requested transmit levels, although humpback calls with greater low frequency energy were at the lower end of this range.

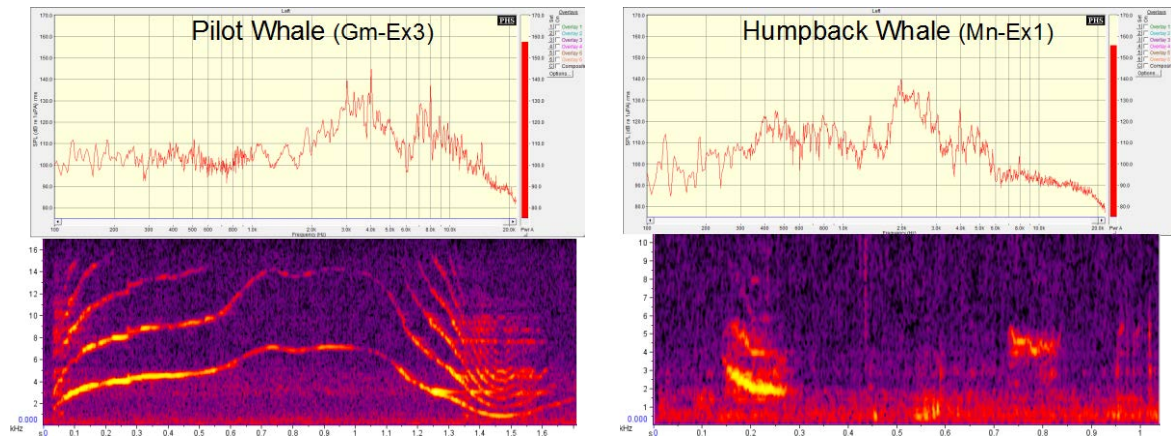


Figure 1.7. Test stimuli calibration measurements at 1 m from the LUWBUSS. Requested source levels were 160 dB re: $1\mu\text{Pa}\cdot\text{m}$ in both cases. Measured source levels were 158.1 and 156.1 dB re $1\mu\text{Pa}\cdot\text{m}$ for these pilot whale and humpback whale exemplars.

We measured each test stimulus during playback experiments using the calibrated hydrophone and analysis software, although monitoring hydrophones were deployed approximately 4 m away from the sound source (Figure 1.8).

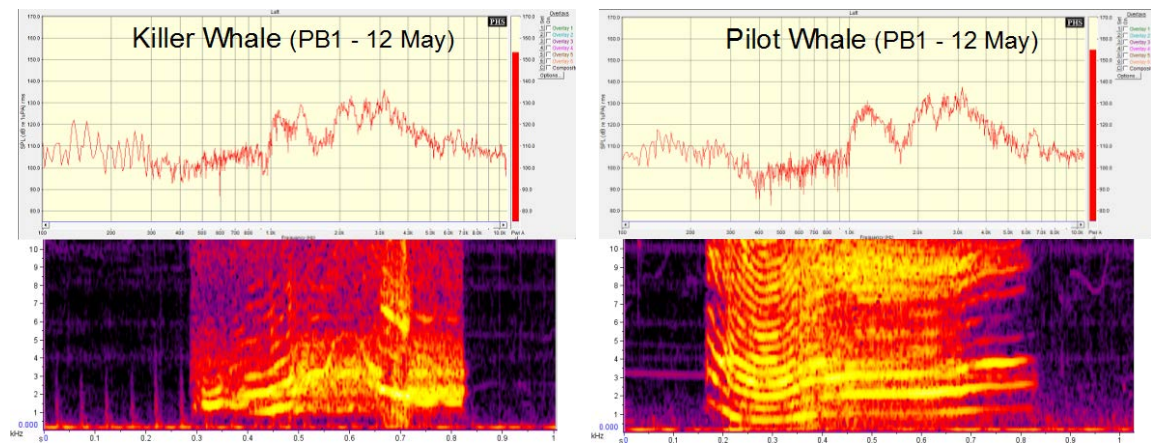


Figure 1.8. Test stimuli measured at ~ 4 m from the LUWBUSS during playbacks on 12 May 2012. Requested source levels were 160 dB re: $1\mu\text{Pa}\cdot\text{m}$ in both cases. Measured source levels were 152.9 and 156.1 dB re $1\mu\text{Pa}$ for these individual elements of killer whale and pilot whale exemplars.

Chapter 2: Short-finned pilot whales and Risso's dolphins respond strongly and divergently to non-linear killer whale calls

2.1 Introduction

As noted above, strandings of beaked whales linked to training exercises employing MFAS have raised considerable conservation concern (Cox et al. 2006; D'Amico et al. 2009; Fernández et al. 2005; Hohn et al. 2006; Parsons et al. 2008). Beaked whales have garnered most of this attention, but other cetacean species have stranded coincidentally with naval exercises (Hohn et al. 2006; Nowacek et al. 2007). A considerable body of research (e.g. Southall et al. 2012; Goldbogen et al. 2013; DeRuiter et al. 2013; Miller et al. 2014; Antunes et al. 2014) has been devoted to understanding the impact of MFAS using controlled exposure experiments, but the underlying drivers of such responses have remained obscure, in part because MFAS signals are produced at frequencies lower than the best hearing of many toothed whales (e.g., Tyack et al., 2011) and above those of many baleen whales (e.g., Goldbogen et al. 2013). Zimmer and Tyack (2007) first noted the similarities between the acoustic signals used in MFAS and the social sounds made by mammal-eating transient killer whales (*Orcinus orca*). This led to the hypothesis, described above, that the strong aversive responses may reflect an anti-predatory behavior in which animals are responding to sonar signals that they perceive as killer whale sounds (Tyack 2009a; Tyack et al. 2011).

If some odontocetes categorize, or respond to, MFAS as if they were the calls of a predator, we should be able to predict their responses based on knowledge of their anti-predator strategies, if known, or make inferences into these strategies based on knowledge of their social behavior. Once a predator is detected, potential prey may respond by moving away (flight), through group or individual defense (fight), or some combination of these strategies (Stanford 2002). The results of several controlled exposure experiments (CEEs) on free-ranging cetaceans, primarily using anthropogenic sources of sound, have supported the anti-predator hypothesis. For example, a Cuvier's beaked whale responded to simulated MFAS by stopping vocalization, rapid directed movement away from the sound source, and extended dive duration with slow ascent, with some of these behavioral changes lasting well after the end of the exposure (DeRuiter et al. 2013). The apparent flight response observed in beaked whales may place individual animals under physiological risk under certain exposure circumstances (Fahlman et al. 2014; Tyack et al. 2011). Avoidance response to simulated MFAS has been recorded in several other species of cetaceans (Stimpert et al. 2014; Miller et al. 2014; Goldbogen et al. 2013; Maybaum 1993), but the strength and duration of this response, relative to exposure, varies across and within species. Importantly, not all species exhibit a flight response. In particular, pilot whales typically do not exhibit silencing and avoidance behavior after exposure to MFAS or the sounds of predators (Miller et al. 2012; Tyack 2009a). The response of pilot whales to simulated MFAS signals in the Bahamas BRS (Southall et al. 2008) was more reminiscent of a social defense strategy, which included elevated vocalization rate and increased group cohesion (Tyack 2009a). Taken together, these results suggest that sociality (and specifically the social nature of anti-predator behavior) might mold the response of cetacean species to MFAS signals.

Protection from predators is one of the most important factors promoting the evolution of sociality in mammals (Connor 2000). Group living can provide protection to an individual in a variety of ways. Detection of predators is more effective in larger groups and an individual in a large group has a decreased probability of being attacked than an individual in small

group (Stanford 2002). Increased vigilance and diluted predation risk is often cited as a factor promoting sociality in birds and primates (Rubenstein 1978). Anti-predator defense can include a variety of behavioral tactics including herding, confusion tactics, alarm calls, fleeing, and/or confronting the predator with mobbing behavior (Rubenstein 1978). Increasing group cohesion may lead to predator confusion (Milinski 1984), and fleeing in a coordinated manner can make it more difficult for a predator to target any one individual from the group (Alcock 2005). Alarm calls, such as vocalizations emitted in the presence of danger (Caro 2005) can serve a variety functions, including conveying information about the identity of a predator and location (Seyfarth et al. 1980), and/or signaling awareness of the predator (Zuberbühler et al. 2009). Alarm calls can also be used to recruit conspecifics to engage in mobbing behavior in both mammals and birds (Curio et al. 1978; Tamura 1989).

Actual predation events are extremely rare for long-lived marine mammals and, consequently, difficult to observe. As a result, many researchers have conducted playback studies with predator sounds to test the response of these animals to the risk of predation. Most playback experiments involving marine mammals have used killer whale (*Orcinus orca*) calls as the experimental stimulus. Killer whales occur in several ecotypes which may act as predators or potential competitors of other marine mammals. Playbacks of the calls of fish-eating killer whales to long-finned pilot whales (*Globicephala melas*) resulted in increased group size and movement towards the sound source (Curé et al. 2012). In contrast, harbor seals (*Phoca vitulina*) responded strongly to the calls of mammal-eating killer whales and unfamiliar fish-eating killer whales. Interestingly, however, the harbor seals did not respond to the calls of familiar fish-eating killer whales, suggesting that they were capable of discriminating between the calls of different ecotypes of killer whales (Deecke et al. 2002). This suggests that harbor seals successfully categorized the calls of different killer whale ecotypes, based on the perceived risk of predation, and responded appropriately. Solitary male sperm whales (*Physeter macrocephalus*) stopped foraging and increased vocalization rates in response to the sounds of mammal-eating killer whales (Curé et al. 2013). Humpback whales (*Megaptera novaeangliae*), which were predicted to respond to killer whales by aggression (Ford and Reeves 2008), responded to playbacks of mammal-eating killer whale with strong avoidance behavior (Curé et al. 2015). Behavioral context is critical in such experiments and, in the latter case, the observed flight response may have occurred because the humpback whales perceived the predator as a distant threat (Curé et al. 2015).

Here we report the results of an experiment designed to address the role of sociality in mediating the anti-predator response of odontocete cetaceans by performing playbacks to two closely related species with different patterns of social organization. In our experiment we measured individual and social response of short-finned pilot whales (*Globicephala macrorhynchus*) off North Carolina and Risso's dolphins off California (*Grampus griseus*) to the sounds of mammal eating killer whales.

There are no published accounts of killer whales preying on our two focal species, but both have been found in the stomachs of killer whales (Jefferson et al. 1991). Killer whales have been observed attacking and killing long-finned pilot whales (Bloch and Lockyer 1988; Donovan and Gunnlaugsson 1989). Even rare predation attempts can exert a significant selective force on social behavior, particularly amongst long-lived species such as primates and marine mammals (Connor 2000; Isbell 1994; Marino 2002).

Short-finned pilot whales are highly social odontocetes found in tropical and subtropical waters throughout the world. These pilot whales typically occur in small, stable social groups

that frequently coalesce into larger aggregations. Like humans and killer whales, female short-finned pilot whales exhibit reproductive senescence (Kasuya and Marsh 1984). The evolution of such an unusual trait reflects permanent social bonds amongst related individuals and females, at least, are believed to exhibit philopatry to their natal group (Alves et al. 2013b; Heimlich-Boran 1993). The extremely cohesive nature of their social structure has been suggested as an explanation of frequent mass strandings of this species that can result in the death of all group members (Olson 2009). Field observations in Hawaii suggest that only adult males disperse from their natal groups (Mahaffy et al. 2015). Closely related long-finned pilot whales, whose social structure has been better studied, live in permanent family groups from which neither males nor females disperse (Amos et al. 1993; de Stephanis et al. 2008).

In well-studied populations near Tenerife, (Heimlich-Boran 1993), Madeira (Alves et al. 2013b), and Hawaii (Mahaffy et al. 2015) individual short-finned pilot whales exhibit long-term patterns of social association. In Madeira, pilot whales show differential patterns of residency and site fidelity (Alves et al. 2013b; Mahaffy et al. 2015), but genetic analysis indicates this differential site fidelity is due to social philopatry and not genetic differentiation (Alves et al. 2013b). Genetic analysis of stranded long-finned pilot whales in New Zealand revealed multiple unrelated matrilineal lines occurring in association with each other (Oremus 2008).

Risso's dolphin's (*Grampus griseus*) are closely related to pilot whales and are classified together in the sub-family Globicephalinae (LeDuc 2009). Like pilot whales, they are medium-sized odontocetes found in tropical, subtropical and temperate waters throughout the globe. The social structure of Risso's dolphins has not been as well studied as that of pilot whales, but their social organization is characterized by more fluidity. In Tenerife, both male and female Risso's dolphins leave their natal pods (Visser 2014) and genetic analysis of Risso's dolphin groups show low overall levels of relatedness (Gaspari 2004). The structure of the Tenerife population shows similarities to the fission-fusion model of social organization, with some individuals exhibiting no stable patterns of association (Visser 2014). However, most of the population is organized into pods, with loose associations of sub-adults and more stable relationships among pairs or clusters of older animals (Visser 2014). These groups are stratified by sex and maturity, with stronger associations among adult males and females (Hartman et al. 2008; Visser 2013).

We conducted field experiments to document the response of these two species to the sounds of mammal-eating killer whales. We predicted the response of these two species based on our knowledge of their social behavior. Specifically, we predicted that the pilot whales would respond to the calls of a potential predator by increasing social cohesion and vocalization rate. In contrast, we predicted that Risso's dolphins would move away from the sound source and reduce their vocal activity.

2.2 Materials and Methods

We developed the experimental protocol at the Stimulus Design Workshop in 2012 (as described in Chapter 1). The field trials were designed to present realistic scenarios in which focal animals would detect the presence of a predator at a moderate (hundreds of meters) distance. Consequently, we used representative source levels based on field measurements of killer whale social calls, instead of trying to maximize the received level of sounds on

experimental animals. We used positive and neutral control stimuli that were deliberately balanced in terms of sound output to ensure that any differential responses were not a function of relative sound level. In addition, the stimuli were of short duration, to provide a cue that was just sufficient to elicit the natural response(s) of the focal animals and to reduce the likelihood that they would determine that no predator was actually present.

Field Sites

We conducted playback experiments with pilot whales off Cape Hatteras, 50 km east of Oregon Inlet, North Carolina, and with Risso's dolphins off the coast of Southern California near Catalina Island. We performed all playbacks in Beaufort Sea States of 0- 3 so that we could observe behavioral responses of the focal animals and their groups at the surface.

Playback Stimuli

The calls of mammal-eating killer whales constituted the *experimental stimulus*. Good quality recordings of the calls of mammal-eating killer whales are rare, so we used representative exemplars from the population of mammal-eating killer whales in the Pacific Northwest (see Deecke et al. 2005). We used conspecific calls as *positive controls* in both field trials. In the pilot whale trials, we used calls that are produced during ascent to the surface from foraging dives in a different population (Jensen et al. 2011), but we expected that focal animals would respond to these exemplars with less urgency than to the calls of predators, or perhaps not at all (*sensu* Deecke 2006). The humpback whale (*Megaptera novaeangliae*) calls were *true controls* – we did not expect the focal pilot whales or Risso's dolphins to respond to these familiar, non-threatening exemplars in any way. The use of a true control allowed us to assess whether there were any artifacts created by our sound source or field protocol that could influence the response of the focal animal to the experimental stimuli (i.e. artifacts that might elicit a response due to the novel nature of the stimulus, regardless of its behavioral context).

Thus, in each playback trial, a focal animal was presented with three sets of acoustic stimuli, or *exemplars*: (1) calls of mammal-eating killer whales recorded from DTAGs off the Pacific coast of the U.S. and Canada (the sound of potential predators, Figure 2.1); (2) pilot whale social sounds recorded using DTAGs in Tenerife, Spain or Risso's dolphins recorded with DTAGs off the coast of Southern California (the sound of conspecifics, Figure 2.2 and Figure 2.3); and (3) humpback whale social sounds recorded with DTAGs from the Stellwagen Bank National Marine Sanctuary, off Cape Cod, Massachusetts (true controls, Figure 2.4). Due to the limited availability of recordings, our conspecific calls used in Southern California came from the same population of Risso's dolphins.

We generated all exemplars from high signal to noise recordings and normalized them to have an equivalent maximum RMS voltage using a 200 ms RMS window. We used SpectraPlus and MATLAB tools to measure the relative broadband RMS levels of the signal and normalized using Adobe Audition to ensure output levels were balanced across all test stimuli. We then confirmed test signal levels again in SpectraPlus and MATLAB to ensure that relative output levels were within 1 dB across all test stimuli. Each exemplar was then transmitted through the LUWBUSS software to ensure that signals sent to the transducer elements retained signal integrity in both time and frequency domains across the operating frequency band.

Each playback trial consisted of three discrete playback sequences involving seven identical exemplars from one of the three species (killer whale, humpback whale, and conspecific (Risso's/pilot whale)). Each playback sequence was spaced 30 minutes apart and included

seven repetitions of the same exemplar. Each exemplar (calls of killer, pilot whales or Risso's dolphins, and humpback whales) was unique and used only once in trials with each focal species, to avoid pseudo-replication (Deecke 2006). That is, we used the same set of exemplars for both Risso's dolphins and pilot whales, but the same exemplars were not used for multiple subjects within the same species.

We selected exemplars randomly without replacement using 'randperm' in MATLAB, with one important exception. In the last year of the experiment, we restricted our selection of killer whale calls to biphonic signals, because of the strong response observed to these call types by both focal species in prior trials.

Thus, each stimulus set consisted of seven repeated exemplars with a four-second interval between each call. We selected the sequence in which stimuli sets were presented (*e.g.* pilot whales, followed by killer whales, followed by humpback whales) randomly using 'randperm' in MATLAB (MATLAB 2012). Each exemplar was relatively short in duration (~0.5-1 sec) and the entire presentation of an exemplar set lasted no more than 34 seconds. Spectrograms of all exemplars were generated in Adobe Audition Creative Cloud 2015 and are shown below (Figs. 2.1 to 2.3).

The requested source levels for all exemplars were normalized to 168 dB re 1 μ Pa-m as described above. We chose this source level to match naturally occurring source levels for killer whales and used balanced levels for playbacks of other species to ensure that all stimuli were presented at equivalent levels, to avoid cues based solely on level (Deecke 2006).

Finally, each playback trial occurred at a predetermined time and not in a contextual fashion. Thus, we did not wait for a focal animal to enter a particular behavioral state (resting or foraging, for example) before starting the trial.

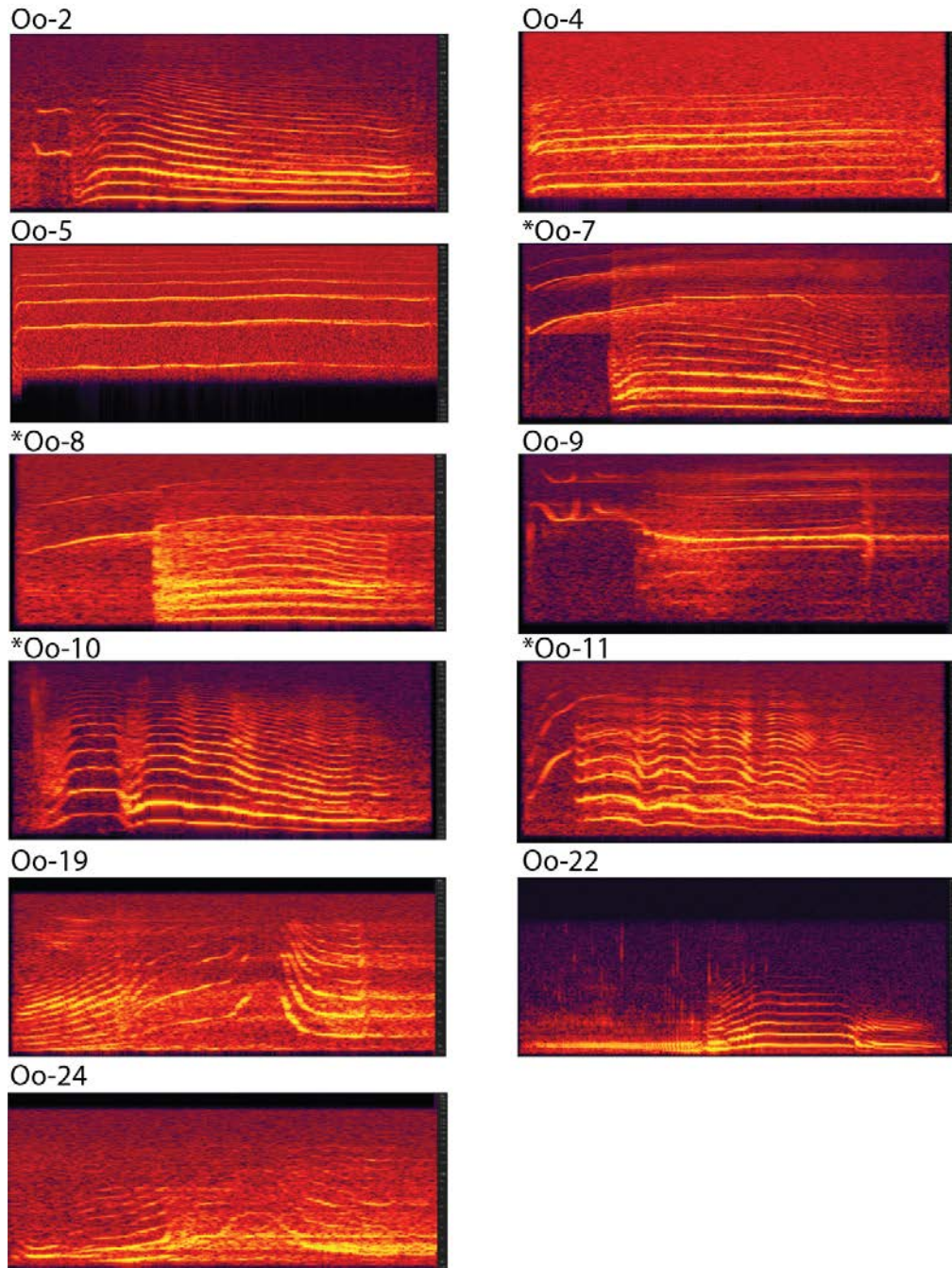


Figure 2.1 Spectrograms of calls from mammal-eating killer whales used in playback experiment with short-finned pilot whales and Risso's dolphins *denotes that a strong response was observed during field trials.

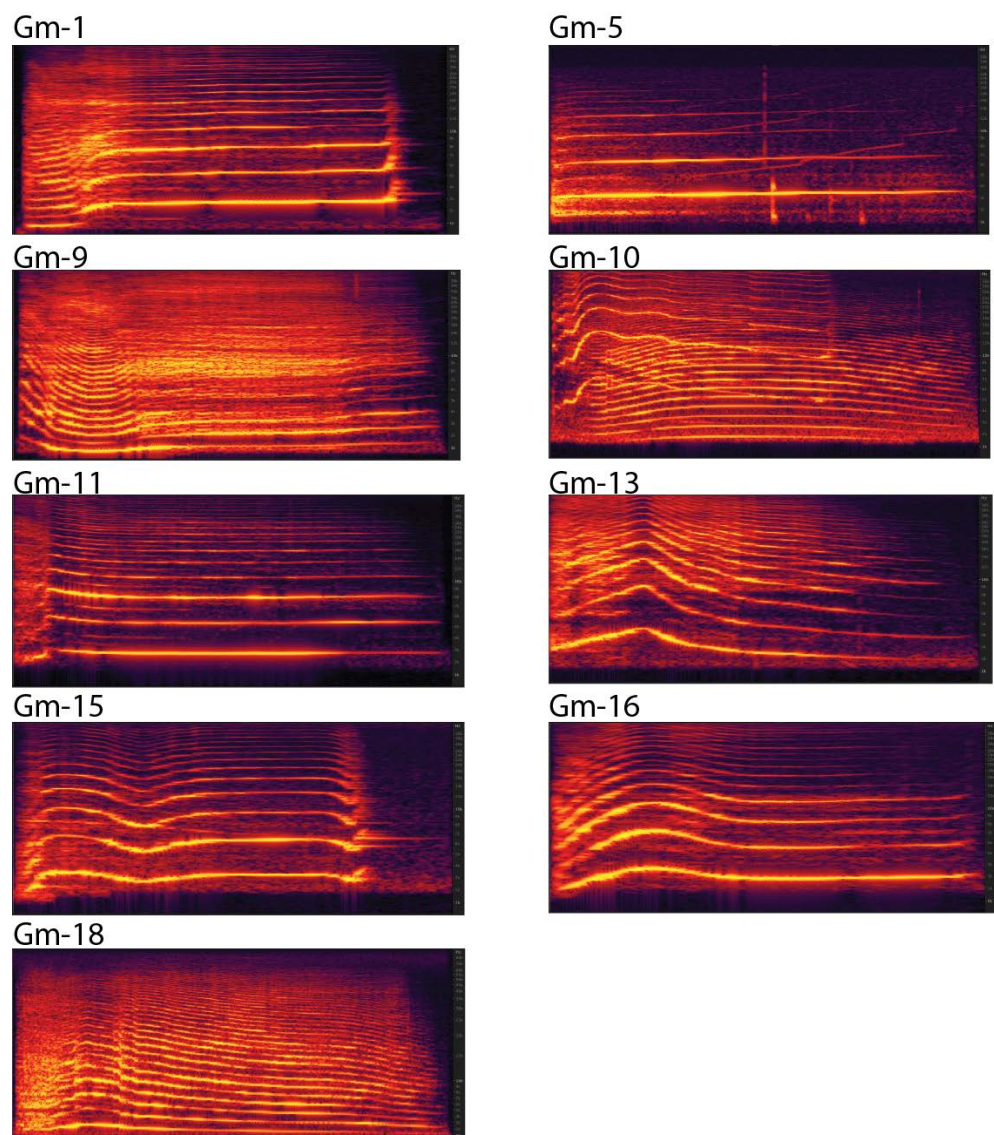


Figure 2.2. Spectrograms of short-finned pilot whale calls from Tenerife used in playback experiment with short-finned pilot whales off Cape Hatteras.

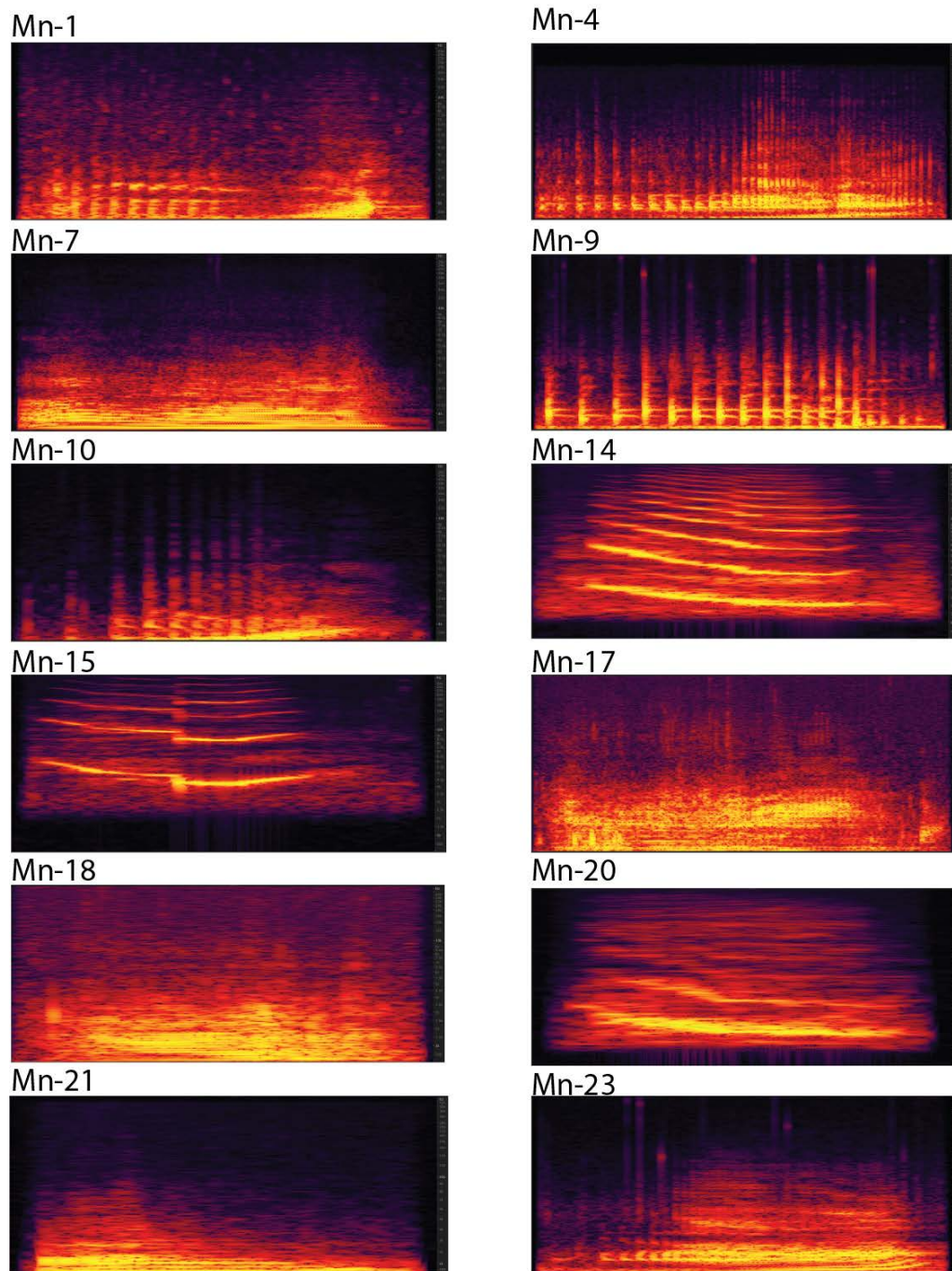


Figure 2.3. Spectrograms of humpback social sounds from Stellwagen Bank used in playback experiment with short-finned pilot whales and Risso's dolphins.

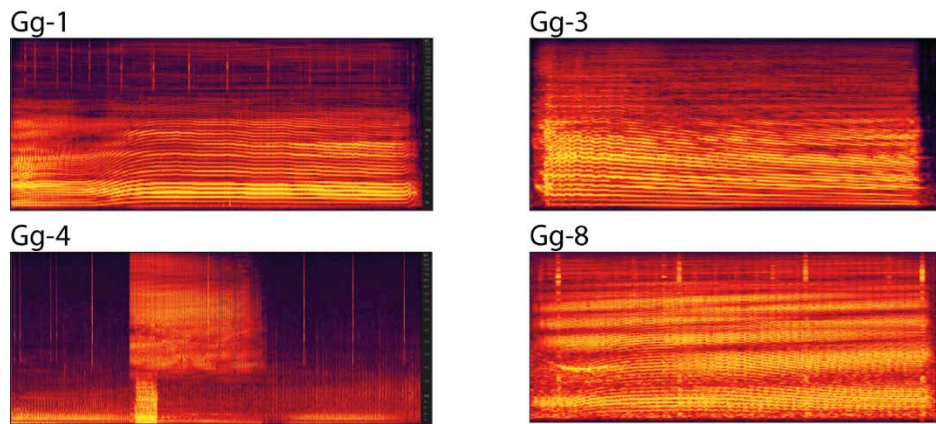


Figure 2.4. Spectrograms of Risso's dolphin calls from southern California used in playback experiment with Risso's dolphins off Catalina Island.

Experimental Protocol

In each field trial we employed two vessels: a *Source Vessel (SV)*; and a small Rigid-Hulled Inflatable Boat as the *Observation Vessel (OV)*. We approached each group in the OV and selected a large, well-marked pilot whale or Risso's dolphin and attached a Version 2 or 3 DTAG (Johnson and Tyack 2003) to the dorsal fin or dorsal surface with an anticipated deployment time of four hours. We avoided tagging females with dependent calves and, as a condition of our permits, we did not work with groups of either species that contained neonates.

Once the focal whale was tagged, we obtained photographs of the tag attachment and assessed the quality of VHF signals received from the tag. Based on these observations and other factors (*e.g.*, weather), we assessed the potential for completing the full experimental protocol. We began the experiment with a 60-minute *pre-exposure* period of observation. During this period, the SV remained several kilometers away from the focal animal, with all active acoustic sources turned off. Observers on the OV recorded the behavior using a point sampling protocol designed to provide information on the behavioral state of the tagged animal, including several measures of social cohesion for the focal group.

Following the pre-exposure period, the operator on the SV contacted observers on the OV to ensure that no neonatal animals were in the group. Once experimental and required mitigation conditions were met, the SV moved into a position approximately 200-500 m (but not directly ahead of) from the tagged whale. The operator on the SV deployed the sound source, confirmed no animals were in proximity to the sound source, and conducted the first playback trial, as described above. Observers on the OV were blind to the playback sequence and identity of the exemplar, to ensure that we avoided any potential for observer effects, (Deecke 2006). The initial playback was followed by a 30-minute period of observation before the process was repeated for a second and then again for the third set of exemplars. After the final playback, we continued to collect behavioral observations until the tag jettisoned from the whale. We attempted to obtain a remote biopsy sample of skin from focal pilot whales (but not for Risso's dolphins, due to permit issues) immediately after we recovered the tag. The biopsy samples allowed us to determine the sex of the focal whale.

Processing Received Stimuli

We isolated playback signals on the DTAG records and analyzed these signals in several steps. After locating and isolating individual stimuli, we ran custom MATLAB scripts on each stimulus signal. These scripts account for the gain settings and calibrations of individual DTAGs and calculate the received levels (RL) and signal to noise ratio (SNR) for each of the playback stimuli (Table 2.4). We generated maximum levels from measurements made in 200 ms windows during the duration of the playback. Importantly, we used transient elimination algorithms on all signals, which excludes energy from short, intense sounds such as echolocation clicks and allows for accurate calculation of the RLs (as described in Tyack et al. 2011). We calculated levels for a single broadband value, resulting in 19 RL 1/3-octave measurements and a single broadband measurement. A high-pass filter on the DTAGs ensured that low-frequency flow noise did not contribute to this measurement. We present all measurements in (RMS) units of dB re: 1 μ Pa calculated with the 200 ms window.

Analysis of Movement

We first assessed each playback qualitatively by plotting tag data, including the acoustics spectrogram, flow noise (noise power at 500 Hz band-pass filtered with a 2-pole Butterworth filter), overall dynamic body acceleration (ODBA), depth, and heading for the 30 seconds before during and after each playback (Figure 2.3 and Figure 2.4). We chose 30-second time periods to match the duration of the playbacks. Flow noise and ODBA were calculated following procedures outlined in prior studies (Qasem et al. 2012; Simon et al. 2009). After observing a strong pattern of heading changes and increased ODBA associated with playbacks of biphonic calls (containing two fundamental frequencies) from mammal eating killer whale calls, we decided to group killer whale calls into monophonic and biphonic calls for further analysis.

We estimated mean ODBA in 30-second time steps against four treatments: baseline, before, during, and after, for each call type with a Gaussian General Estimating Equation (GEE) using the geepack package (Højsgaard et al. 2006) in R statistical software (R Core Team 2014). GEEs are used to determining population-averages when the responses are not independent. GEEs make population level inference and allow for making within-subject correlation. GEEs have been used in a number of other playback experiments with cetaceans to test stimulus effect (Curé et al. 2012). We ran models with an independent and autoregressive correlation structure and used the ANOVA method to compare each model by Wald tests. In each case the independent correlation structure was determined to be a better model. Each treatment was compared to the baseline using 95% confidence intervals derived from a parametric bootstrap of 10,00 iterations on the fit parameters of the GEE. For the bootstrap we assumed a multivariate normal distribution with means equal to the estimated parameters from the model and the variance-covariance matrix from the fit model.

We estimated the focal animal's position and heading at each available surfacing using range and bearing from the *OV*, combined with estimates of the vessel's position from an on-board GPS unit. We interpolated the path of the focal animal for the duration of the experiment by creating straight-line tracks between each of these points. Using this interpolated path, we calculated the distance between the focal animal and the sound source immediately prior to the playback and for the 30 minutes following each playback. We then determined the bearing between the focal animal and the sound at the time of the playback using this track. We then evaluated whether the animal changed its heading relative to the source by running a circular two sample t-test on the heading data collected on the DTAG for the 2 minutes before and after each playback (Berens 2009).

Analysis of Social Calls

We estimated call counts on the DTAG record in the baseline period (10 minutes before any stimulus) and for five minutes before and after each stimulus. We did not analyze call counts during the playbacks due to the high levels of background noise (flow-noise and splashing) which occurred on a number of the playbacks. We identified feeding buzzes and clicks following methods described in Soto et al. (2008). In the present analysis, we incorporated all calls that were not feeding buzzes or clicks, which included whistles, burst pulses, social buzzes, and rasps. These calls were binned into 30-second time steps and we analyzed with a Poisson GEE using the geepack package (Højsgaard et al. 2006) in R statistical software (R Core Team 2014). We ran models with an independent and autoregressive correlation structure and used the Anova method to compare each model by Wald tests. In each case, the independent correlation structure was determined to be a better model. Each treatment was compared to the baseline using 95% confidence intervals derived from a parametric bootstrap following the same procedures described above.

2.3 Results

The LUWBUSS system performed according to specification, with maximum received levels of the various playback exemplars received on DTAGs ranging from 102-137 dB (Table 2.1). In three of 41 exemplars, signals were not detected on the DTAG at the time they were presented. The degree of variation we observed in received levels was expected, given that we used natural source levels, and due to propagation effects and the tagged whale's range from the source and position in the water column (Madsen et al. 2006). Furthermore, the received level recorded on the tag can be affected by the orientation of the animal relative to the source. For example, the received level will be reduced if the animal's body or the body of another whale is shadowing the tag.

Table 2.1. Maximum RMS (dB re: 1uPa) broadband received levels (Max RL) for all playbacks. X denotes playback exemplars that were not detected on the tag acoustic record. An asterisk denotes that the DTAG jettisoned before the call was played.



In total, we completed nine complete playback sequences that included presentation of all three sets of stimuli to pilot whales (Table 2.2). We also completed three complete playback sequences and one partial sequence (two playbacks) to Risso’s dolphins (Table 2.3). Seven of the exposed animals (five pilot whales and two Risso’s dolphins) displayed strong and unequivocal responses to the calls of mammal-eating killer whales, while the other seven did not. The response of both pilot whales and Risso’s dolphins during the playback included increases in speed, heading variance, and ODBA (Figure 2.5 and Figure 2.6). After the playback, pilot whale call rates increased and the focal pilot whales and their groups made directed movement towards the sound source. Risso’s dolphins exhibited no measurable change in call counts, but made rapid directed movement away from the sound source.

Of the seven strong responses we observed, four of the five pilot whales and one of the two Risso’s dolphins occurred in response to biphonic calls of mammal-eating killer whales. One monophonic killer whale call (Exemplar 10 - Figure 2.1) also elicited a strong response during playbacks to both pilot whales and Risso’s dolphins. We observed no measurable response to any of the humpback or conspecific calls.

Table 2.2. Playback calls, stimulus order, and group context for each pilot whale playback trial.

Pilot Whales ID	
Gm14_178b	ion of several hundred during the experiment

Table 2.3. Playback calls, stimulus order, and group context for each Risso’s dolphin playback trial.

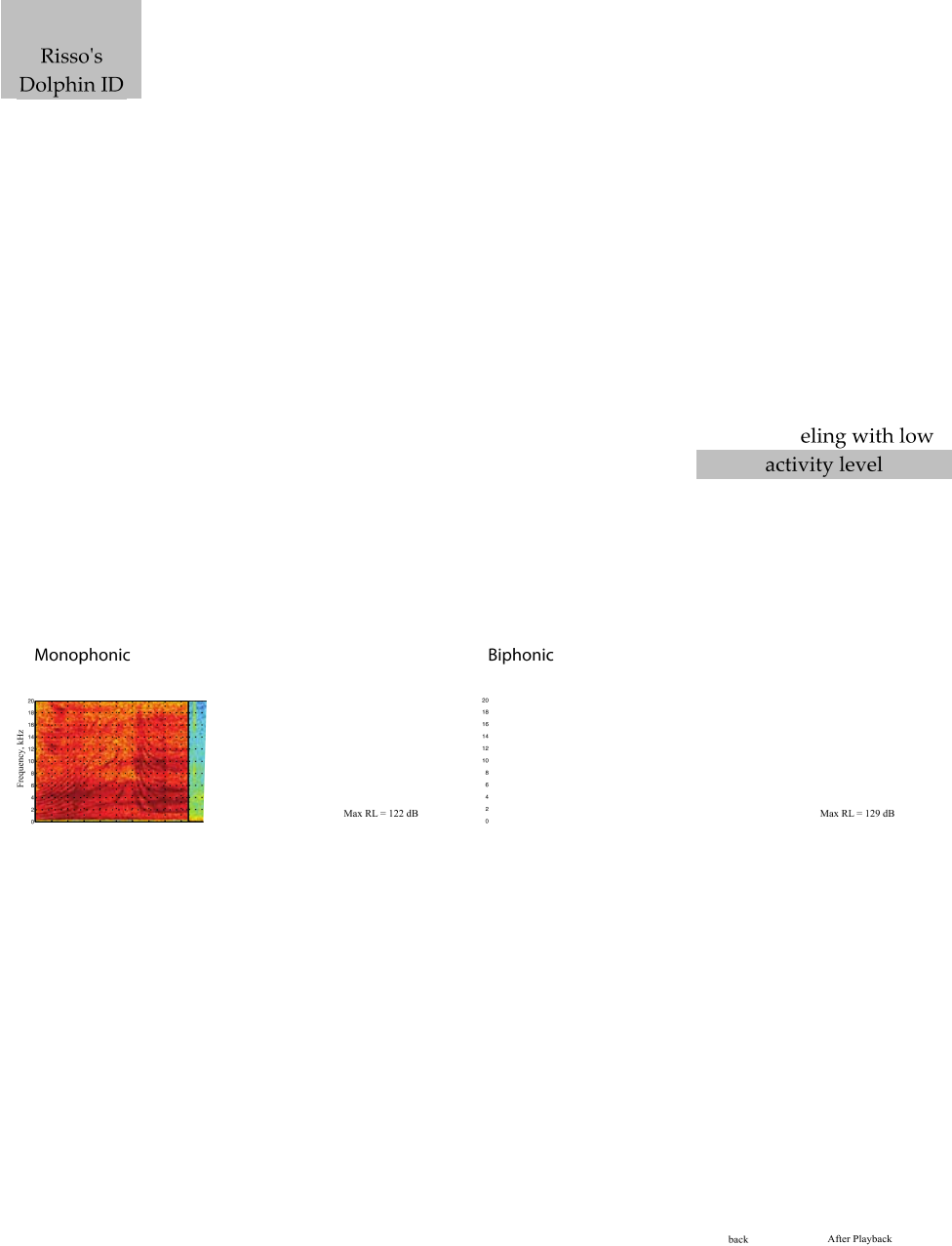


Figure 2.5. Examples of a lack of reaction (left) and a strong reaction (right) of short-finned pilot whales to playbacks of monophonic and biphonic mammal-eating killer whale calls. The reactions included increased flow noise, ODBA and heading variance. Each panel displays a 30-second period before, during and after presentation of a killer whale call and provides values for: (A) transmitted and received signals; (B) spectrogram of the acoustic record; (C) flow noise, which is a proxy for the speed of the tagged animal; (D) depth profile of the tagged animal; (E) ODBA, which is a proxy for movement of the tagged animal; and (F) circular plots of heading of the tagged animal.

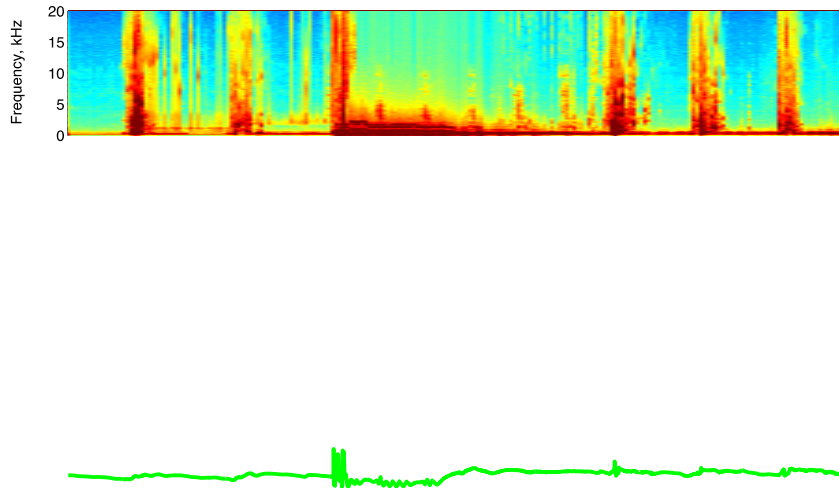


Figure 2.6. Response of Risso's dolphin Gg13_228b to playback of a mammal-eating killer whale call. Similar to the response seen in pilot whales, we observed an increase in flow noise, ODBA and heading variance during presentation of the killer whale call. The figure displays the 30 seconds before, during and after the playback and displays: (A) spectrogram of the acoustic record; (B) flow noise, which is a proxy for the speed of the tagged animal; (C) depth profile of the tagged animal; (D) ODBA, which is a proxy for movement of the tagged animal; (E) pitch and fluke strokes by the tagged animal; and (F) heading of the tagged animal.

Observational data

A large number of values were missing from our surface behavioral observations, as the focal animals were often submerged and thus unavailable, so we were unable to perform any robust statistical analysis on the observational data. Nevertheless, we can use these observations to provide a qualitative description of the response of focal animals and their groups to the playbacks. Following the playback of biphonic killer whale call to pilot whale Gm12_125a, for example, two sub-groups of whales moved quickly to coalesce into a single, very tight group, with almost all whales in physical contact. The group then dove in unison, moving towards the sound source. We witnessed a similar response following the playback to pilot whale Gm14_145a; the focal group contracted, with almost all of the whales in physical contact. The group then moved in a coordinated and directed manner towards the sound source. In contrast, playbacks of most monophonic killer whale calls evoked little or no obvious response from the focal animal or its group.

We also observed strong responses following the playbacks of biphonic killer whale calls to Risso's dolphins Gg13_228b and Gg14_222a, in which sub-groups clustered together into a tight formation over the course of several minutes following exposure, before making extremely strong directional movement (leaping at high speed) away from the sound source for distances up to 7 miles. Note that, in both cases, the DTAG was shed before or at the commencement of this rapid directional travel. In our experience with this species in southern California, this behavior was extraordinary and observed only after these playbacks of these two exemplars.

Analysis of DTAG data

The general estimating equations (GEEs) for pilot whales demonstrated a number of clear aspects of the behavioral response we observed during playbacks of biphonic killer whale calls. Measured ODBA levels for pilot whales were significantly higher during the playbacks of biphonic than monophonic calls (Figure 2.7). This suggests rapid and variable movement by the tagged animals during exposure to this call type, behavior that would be consistent with either a rapid orienting or perhaps represents a startle response. No other playback type was found to be significantly different during exposure relative to baseline. The large confidence interval we observed during playbacks of monophonic calls is most likely due to the single exemplar (Oo-10) that resulted in a strong response. We observed similar responses in ODBA in playbacks of biphonic killer whale calls to Risso's dolphins, although we do not present those results here in the interests of space.

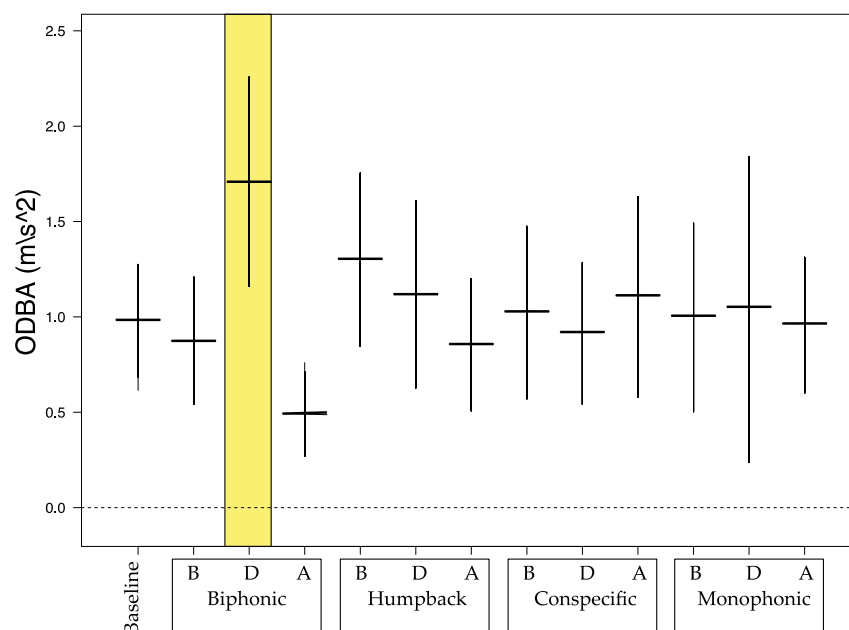


Figure 2.7. Parameter estimates, together with 95% confidence intervals (CI) of Gaussian GEE for ODBA for before, during and after playbacks of various exemplars to short-finned pilot whales. Horizontal lines represent parameter estimates and vertical lines represent the 95% CI derived from parametric bootstrap of the fit parameters of the GEE. ODBA levels during the playback of biphonic mammal-eating killer whale calls (highlighted in yellow) were significantly higher than baseline levels. No other period (before, during or after) for any other stimulus were found to be significantly different from baseline levels.

As noted above, we used social call counts (vocalizations of focal species recorded on the tags) to represent potential changes in social cohesion. We restricted our analysis to periods before and after each playback due to the high levels of background noise (splashing and flow noise) that occurred during some playbacks. For pilot whales, call counts following playbacks of biphonic killer whale calls were significantly higher than baseline levels (Figure 2.8); there was no difference from baseline levels from playbacks of any other call types. There were no significant differences in call counts for Risso's dolphins in any playback condition.

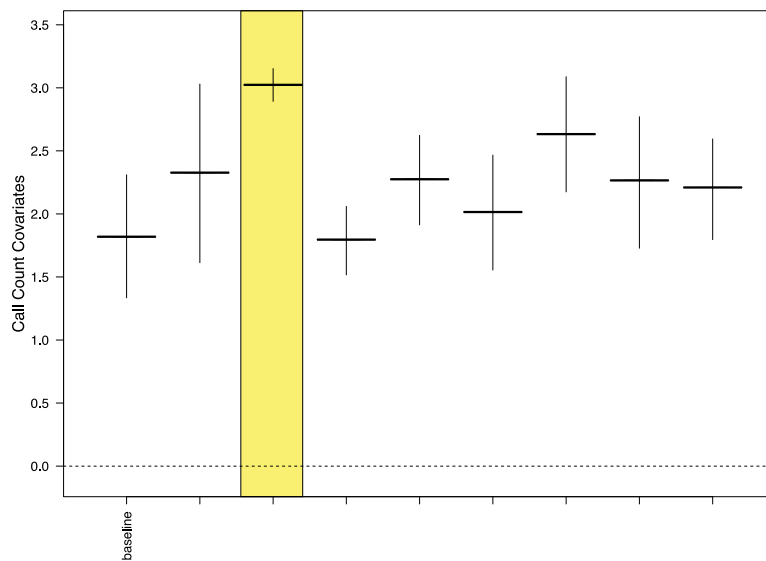


Figure 2.8. Parameter estimates of Poisson GEE of pilot whale call counts before and after playbacks of each stimulus type. Horizontal lines represent parameter estimates and vertical lines represent the 95% CI derived from parametric bootstrap of the fit parameters of the GEE. Call counts following the playback of biphonic mammal-eating killer whale calls (highlighted in yellow) were significantly higher than baseline or before levels.

Below we present ODBA values from individual focal animals for each playback trial involving killer whale calls for pilot whales (Figure 2.9) and Risso's dolphins (Figure 2.10). Playbacks highlighted in yellow involved biphonic killer whale calls. In each case we observed an increase in ODBA during the playback followed by a decrease after the playback. The single playback in green involved exemplar Oo-10, which is a monophonic call, but shares several characteristics with biphonic calls. This exemplar elicited a similar reaction in ODBA for both pilot whales and Risso's dolphins. This pattern of increased ODBA during playbacks was not observed in playbacks of any of the other exemplars.

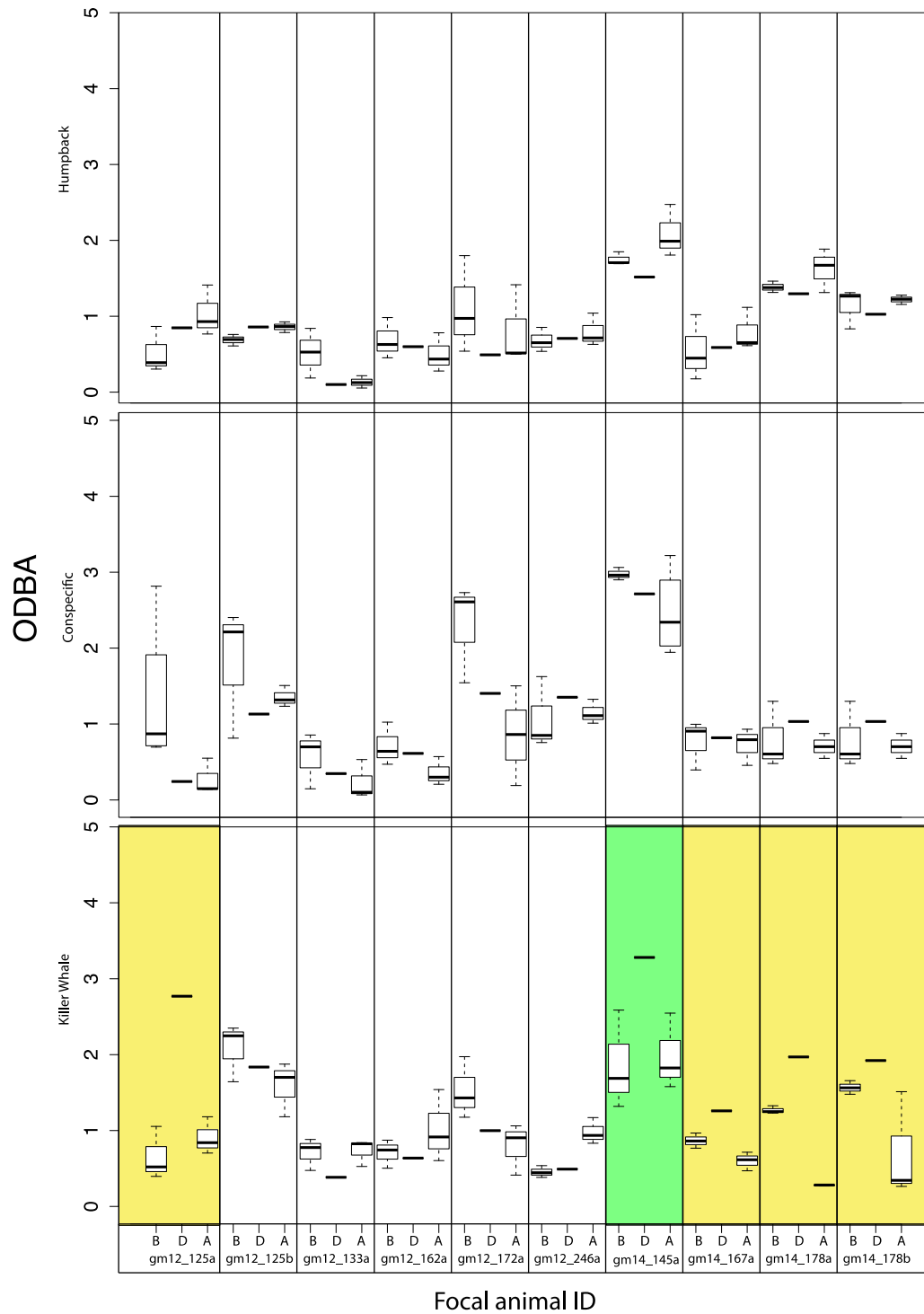


Figure 2.9. Boxplots of ODBA values for 30-second time bins (before, during and after) for three playback stimuli for each tagged pilot whale. Highlighted in yellow are the playbacks of biphonic killer whale calls and in green is the single monophonic call (Oo-10) that elicited a response. All five animals exhibited an increase in ODBA during the playback followed by a reduction in ODBA.

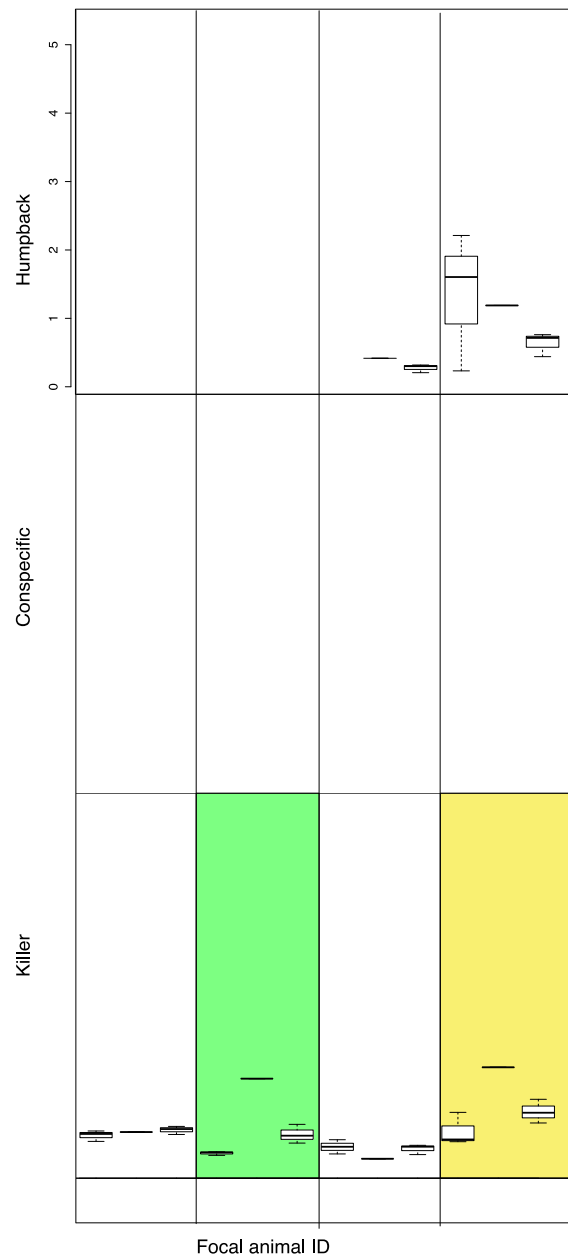


Figure 2.10. Boxplots of ODBA values for 30-second time bins (before, during and after) for three playback stimuli for each tagged Risso's dolphin. Highlighted in yellow is the playback of a biphonic killer whale call and in green is the single monophonic call (OoO-10) that elicited a response. Risso's dolphins displayed a similar response to pilot whales, which included an increase in ODBA during the playback followed by a reduction in ODBA.

We analyzed individual responses to playback trials in terms of physical movement towards or away from the sound source using the estimated heading of focal pilot whales (Table 2.4) and Risso's dolphins (Table 2.5). In both species, we observed no significant difference in terms of distance to the source for playbacks of conspecific calls or humpback whale social sounds. Conversely, playbacks of killer whale calls resulted in significant differences in animal-source distance, with a significant change in tagged animal heading, but only for playbacks involving either biphonic calls or the single monophonic exemplar (Oo-10) sharing certain call features with the biphonic calls. It is important to note that the significant differences measured in responses in these conditions indicated movement toward the sound source for pilot whales (Table 2.4), but movement away from the sound source in Risso's dolphins (Table 2.5).

Table 2.4. Distance between focal pilot whale and sound source during playback trials. Red indicates a significant change in heading, as determined using a two-sample circular t-test on the heading data collected on the DTAG for two minutes before and after each playback.

Distance to Sound Source Following Playback

6a -

Table 2.5. Distance between focal Risso's dolphin and sound source during playback trials. Red indicates a significant change in heading, as determined using a two-sample circular t-test on the heading data collected on the DTAG for the two minutes before and after each playback.

Distance to Sound Source Following Playback

Whale Killer Whale

We also analyzed heading data to investigate potential changes of the orientation of focal animals relative to the sound source for 30 seconds before and 30 seconds after playback of each exemplar. An example of this analysis is provided below for exemplar Oo-10, presented to both a pilot whale and Risso's dolphin (Figure 2.11). The same divergent pattern of response in terms of spatial orientation to the sound source described above is evident here. Both animals made changes to their heading, but the pilot whale oriented towards the sound source and the Risso's dolphin oriented away from the sound source.

Heading Before and After Exposure to MEK Call Oo-10

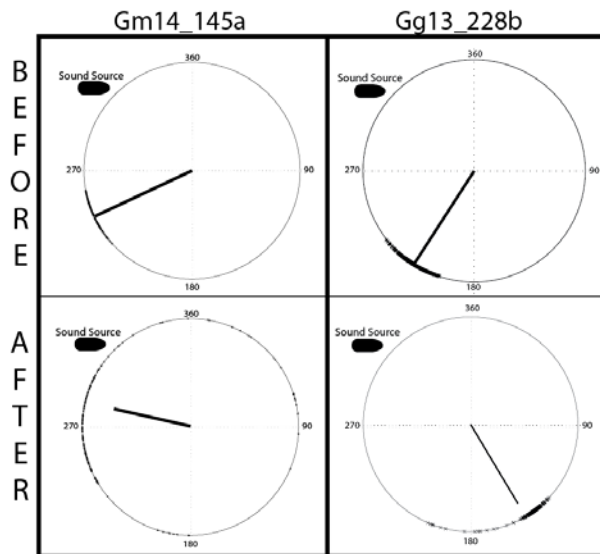


Figure 2.11. Circular plots of heading relative to the sound source for 30 seconds before and after playbacks of killer whale exemplar Oo-10 to a pilot whale (left) and a Risso's dolphin (right). Bearing of the sound source to the focal animal was determined using known location of the sound source and the estimated heading of the focal animal as reconstructed from the focal follow points.

2.4 Discussion

Short-finned pilot whales and Risso's dolphins reacted strongly, but divergently, to playbacks of biphonic calls of mammal-eating killer whales. Neither focal species responded to playbacks of most monophonic killer whale calls or to the calls of conspecifics or humpback whales. The lack of response to the humpback whale calls suggests that there were no artifacts in our playback trails. The GEE showed that both pilot whales and Risso's dolphins increased speed, heading variance and ODBA during and/or after playbacks involving biphonic killer whale calls. In both species, we observed increased cohesion of the focal groups following presentation of the biphonic killer whale calls, but there were clear inter-species differences in their vocal and movement responses. After exposure to the biphonic calls of killer whales, pilot whales increased vocalization rates and approached the sound source. Conversely, Risso's dolphins did not change their vocal behavior, but rather moved in a rapid, directed manner away from the source.

We acknowledge that the samples sizes for both species is small and that the playback exemplars we used do not represent the full range of signals produced by these species. Nor do we fully understand the behavioral contexts in which the calls of mammal-eating killer whales were produced. Nevertheless, given these caveats and within the conditions tested here, we observed clear responses that followed our predictions based on the social behavior of the two focal species. Both short-finned pilot whales and Risso's dolphins responded more strongly to the sounds of potential predators than those of conspecifics and neutral stimuli. Furthermore, we found an interesting and unexpected bi-modal response in responses of both species to killer whale sounds, based on general patterns call structure.

Biphonic calls have been described in all mammal-eating killer whale populations studied to date (Tyson et al. 2007), and their behavioral and contextual usages imply that they function as group identifiers among pods (Filatova et al. 2009). The upper frequency component of these calls is more directional than the lower frequency component, which might allow a receiver to localize the caller based on the relative intensities of the two components in the call (Miller 2006). Biphonic calls tend to have higher source levels than monophonic calls, further supporting the idea that these calls are used for group communication (Miller 2006). Thus, these calls may reflect the presence of a large numbers of killer whales in the area, possibly following cooperative prey capture events, which could explain the strong reactions we observed.

Biphonation and other non-linear phenomena such as sub-harmonics, frequency jumps and deterministic chaos (calls with random or unpredictable elements) are commonly found in alarm calls, and are known to elicit strong reactions in mammals (Fitch et al. 2002; Tyson et al. 2007). The unpredictability of non-linear phenomena in alarm calls may function as a way to prevent habituation (Blesdoe and Blumstein 2014; Fitch et al. 2002). A common example of a human alarm call containing non-linear properties is a screaming baby, which is well known as a difficult signal to ignore. In both mammalian and avian species, the addition of non-linearities to calls, synthesized non-linear sounds, and unfamiliar non-linear biological calls have been shown to provoke strong reactions in animals (Blesdoe and Blumstein 2014; Blumstein and Récapet 2009). All four calls from mammal-eating calls that elicited reactions in the present study contain features that have been described as ‘nonlinear dynamics’ including sub-harmonics, frequency jumps and deterministic chaos.

We do not fully understand why both focal species also reacted to a single monophonic killer whale call. If we consider the time-frequency structure of the 11 killer whale exemplars used in our playback trials, Oo-10 is similar to the calls which elicited strong responses, despite its lack of biphonic content. We are just beginning to explore the responses of odontocete cetaceans to killer whale calls, so these results provide both answers and questions about the acoustic ecology of these animals. As we have reported, three of the four exemplars that elicited strong responses were biphonic calls, but they also contain other acoustic features that may distinguish them from the other exemplars. All of the stimuli that elicited a response contain at least two ‘nonlinear’ features, and some contain three elements (e.g., Oo-7 exhibits frequency jumps, biophonation and possibly deterministic chaos). Determination of whether or not a call contains deterministic chaos requires a lengthy and involved analysis, which was beyond our scope, although the spectrograms do indicate the possible presence of deterministic chaos in calls Oo-2, 7, 8, 9, 10, 11, and 19.

There are many features in these calls beyond those described as ‘nonlinear.’ One feature that is strikingly similar between Oo-10 and Oo-11 is the fairly rapid frequency modulation within a relatively small frequency band; in the spectrogram these modulations create a series of plateaus. In Oo-11 we see this in combination with biphonation and deterministic chaos, whereas in Oo-10 this feature occurs with deterministic chaos and frequency jumps. So, given the strong response we measured when both species were presented with Oo-10, perhaps it is the presence of *multiple* nonlinear features or other features unique to killer whales that elicited such strong responses.

Pilot whale calls share some characteristics with those of killer whales including biphonation and other non-linear phenomena (Sayigh et al. 2013). For example, the exemplar Gm-10 was biphonic, but did not include any other non-linear phenomena. The lack of response of pilot

whales to Gm-10 supports our contention that the behavior following playbacks of killer whale calls was an anti-predator response. There is a large body of literature supporting the concept of an innate identification of predators, and the results of our study suggest that both pilot whales and Risso's dolphins can identify the calls of potential predators *and* discriminate amongst these calls based on structural features.

There were no clear aspects of group size, group composition, or behavioral context that predicted the reactions we observed in pilot whales or Risso's dolphins (Table 2.2 and Table 2.3). Rather, as we have argued above, the responses appeared to result from a differential categorization of calls that reflected the potential risk of predation. In both focal species, these responses occurred in a manner that is consistent with their patterns of social organization. Pilot whales, which live in relatively permanent groups characterized by strong social bonds, responded by increasing social cohesion. Risso's dolphins, with a weaker social structure, exhibited an exaggerated flight response, moving rapidly away from the sound source, in a coordinated manner.

These results do not unequivocally demonstrate that our two focal species have a completely stereotyped anti-predator response or that in all cases the sole determinant of the probability of a response to killer whale calls is the presence or absence of biphonic calls. Nor do our results prove that the strong responses observed to other external stimuli, including MFAS, are necessarily the result of animals categorizing those sounds in the same general class as the calls of predators. However, the responses of both species to signals that share specific call structure is striking, particularly given the small number of playback trials we were able to conduct. Our findings suggest that these animals are performing some type of cognitive categorization, such that social organization of each species modulates the nature of responses that do occur. Furthermore, we suggest that structural similarities of anthropogenic signals such as MFAS, which share features with killer whale sounds, particularly biphonic calls, may be important in terms of response probability and type.

Chapter 3: A Multi-Scale Approach to Understanding Temporal Variation in the Foraging Patterns of Short-Finned Pilot Whales

3.1 Introduction

An essential prerequisite for assessing the impact of anthropogenic disturbance on measures of fitness, such as survival and reproductive success, is an understanding of natural patterns of variation in behavioral states (Viviant et al. 2014). Investigation of variation in behavioral patterns, and of transitions between states, often requires a researcher to define *bouts*, which are periods in which a particular behavior is engaged in frequently, although not necessarily continuously (Bart et al. 2009). For diving mammals that must return to the surface for oxygen at the end of every dive, foraging typically occurs in bouts of dives interspersed with periods of other behavior (Boyd 1997; Luque and Guinet 2007; Mori et al. 2001). Analysis of the duration of foraging bouts, and of variation in this parameter, requires long sampling periods and the ability to differentiate foraging dives from other subsurface behaviors. Studies of bout analysis in cetaceans have lagged behind those of other diving species, such as pinnipeds, due to the inherent difficulties associated with studying these fully aquatic animals in the marine environment (Hooker and Baird 2001).

Despite these challenges, the use of animal-borne biologging tags has revolutionized our understanding of cetacean movement and foraging patterns. The biologging devices now available for use with cetaceans range from archival tags that yield high-resolution data on fine-scale behavior and acoustics (Johnson and Tyack 2003) to satellite-linked sensors that provide relatively coarse positional data over large spatial and long temporal scales (Goldbogen et al. 2013; Schorr et al. 2014). The acquisition of data from these tags are constrained by battery life and the storage space and bandwidth required to transmit the data. As a result, researchers must consider important tradeoffs between data resolution and tag longevity when planning a field program. High-resolution data are often required to accurately define behavioral state (Whitehead 2008), but it is impossible to store such data for long periods or to transmit them over bandwidth-limited satellite systems. Cetaceans range over great distances (Hooker and Baird 2001), so investigation of foraging patterns beyond short periods requires some mode of data telemetry. Satellite-linked time-depth recorders (SLTDRs) relay summarized and compressed data (location, temperature, depth, and dive metrics) through the ARGOS system and can transmit for many months. Recently there have been calls to merge the different modalities of various bio-logging tags to address complex questions of behavioral response over relevant time scales (Goldbogen et al. 2013).

Cetaceans dive for many reasons including foraging, horizontal movement (Fish 2006), predator avoidance (Tyack et al. 2006), and management of blood and tissue gases (Hooker et al. 2012). In studies of pinniped diving behavior, researchers typically classify dives into behavioral categories using metrics such as dive shape and/or bottom duration (Baechler et al. 2002; Boeuf et al. 1988). It is assumed that these aquatic predators maximize profitable foraging time at the bottom of each dive. Simultaneous deployments of additional sensors such as stomach-temperature loggers (Austin et al. 2006), accelerometers (Gallon et al. 2013) and video cameras have been used to ground truth these classification systems. Pinnipeds are well suited for such studies since they return to shore periodically (Ropert-Coudert and Beaulieu 2009), facilitating the deployment and retrieval of multiple archival tags.

Unfortunately, it is difficult, although not impossible, to deploy multiple tags on individual cetaceans. Instead, the predictive power of dive metrics can be tested with the use of high resolution tag data (Viviant et al. 2014). The fine-scale foraging behavior of several species of toothed whales has been described with the use of archival, high resolution, multi-sensor DTAGs (Johnson et al. 2009). Toothed whales echolocate to find prey using low repetition clicks, and produce rapid click trains, often referred to as foraging buzzes, in the terminal phase of prey capture attempts (Johnson et al. 2009). DTAGs provide detailed records of the three-dimensional movement and recordings of the animal's acoustic environment, including the echolocation clicks produced during foraging (Johnson and Tyack, 2003). Records of foraging buzzes, together with records of depth and three-dimensional movement, have been used to identify foraging strategies in several species of cetaceans (Johnson et al. 2004; Soto et al. 2008).

Here we describe the foraging patterns of short-finned pilot whales by combining DTAG and SLTDR records from deployments made off Cape Hatteras, North Carolina. The specific goals of our study were to: (1) evaluate the predictive power of various dive metrics to predict foraging behavior in short-finned pilot whales using high resolution DTAG data; and (2) classify dives from SLTDR records as foraging or non-foraging using these metrics. Our intent was to combine these two types of data streams to analyze long-term foraging patterns and, particularly, to evaluate diurnal variation in foraging behavior and to determine pattern and variation in foraging bouts.

The study area off Cape Hatteras is a particularly dynamic region. Located on the continental shelf break where the Gulf Stream and Labrador Currents converge, the area experiences significant variation in temperatures and flow regimes, as the Gulf Stream meanders east and west and produces a constant stream of transient features, such as frontal eddies that influence the region (Savidge 2004). The area attracts dense concentrations of marine mammals and seabirds, particularly along the shelf break (Best et al. 2012), and commercial and recreational fishing vessels target large predatory fishes in this region year-round (NMFS 2006).

The diet of short-finned pilot whales in this region has been described in only a single study, in which the stomach contents of 27 whales were examined. These whales mass stranded near Cape Hatteras in January 2005 and their stomachs contained a diverse assemblage of small-bodied meso- and bathypelagic cephalopods (Mintzer et al. 2008). At least some of these prey species undertake diel vertical migrations. Based on these observations, we predicted that pilot whales off Cape Hatteras would feed mostly at night when the Deep Scattering Layer (DSL) rises towards the water's surface, making prey more accessible to these air-breathing predators.

3.2 Materials and Methods

We deployed 40 DTAGs and 6 Low Impact Minimally Percutaneous Electronic Transmitter (LIMPET) SLTDR tags on short-finned pilot whales (Table 3.1) along the shelf break off Cape Hatteras (Figure 3.1). All tags were deployed in the summer months; the DTAGs were deployed from 2008 to 2015 and the SLDRs only in 2014 and 2015. We selected larger animals with distinct fins and avoided adult females with dependent calves (Figure 3.2). We used a hand-held carbon-fiber pole to secure DTAGs to the dorsal fin or dorsal surface of

whales from a small rigid-hulled inflatable boat (RHIB). Each DTag was attached to the whale with four 6-cm diameter suction cups and was programmed to release from the tagged whale at a predetermined time. The DTags sampled acoustic data at 96 kHz using a 16-bit analogue-to-digital converter. We sampled the pressure sensor at 50 Hz to generate measurements of the depth of the tagged whale. The LIMPET tags were deployed with a Dan-Inject CO2 rifles and attached to the dorsal fin of each whale. The LIMPET tags used Wildlife Computers SPLASH10-292B sensors, which transmit continuous records of summarized and compressed data on temperature, depth and light for two weeks, before adopting a transmission duty cycle for the remainder of the deployment (Schorr et al. 2014).

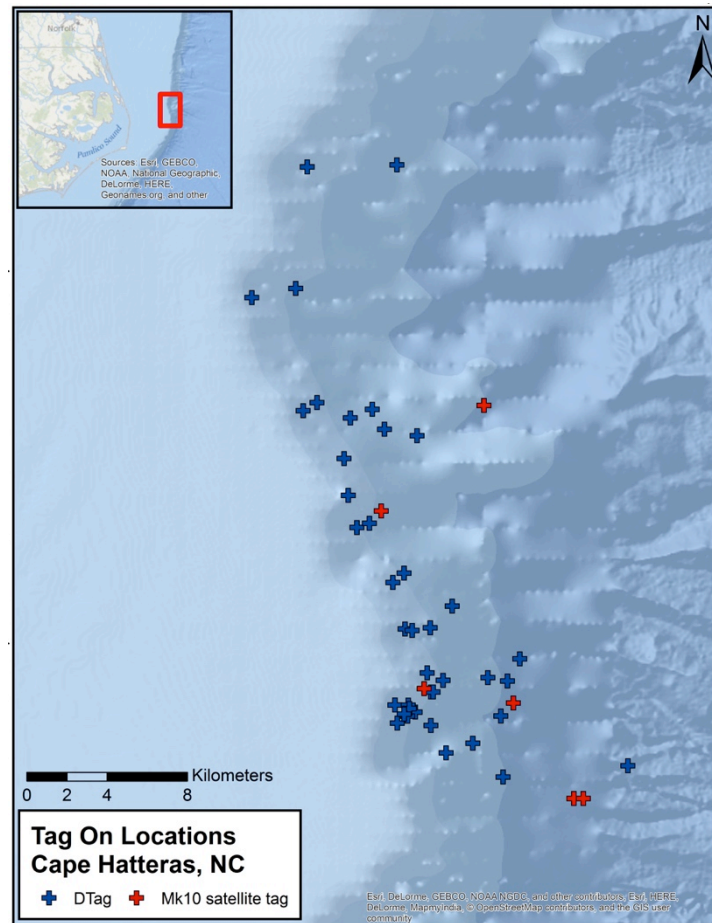


Figure 3.1. Tagging locations for DTAGs and SLTDRs on short-finned pilot whales off Cape Hatteras, North Carolina.

Table 3.1. Deployments of SLTDRs on short-finned pilot whales off Cape Hatteras, North Carolina

Deployment Date	Tag ID	Continuous Duration
5/14/14	Gm_Tag085	14 days
6/11/14	Gm_Tag093	14 days
9/11/14	Gm_Tag098	14 days
9/11/14	Gm_Tag100	14 days
5/16/15	Gm_Tag123	6 days
5/19/15	Gm_Tag127	14 days



Figure 3.2. Images of LIMPET and DTAGs deployed on pilot whales GmTag087 and Gm12_161a off Cape Hatteras, North Carolina.

We performed all data preparation using MATLAB (2012). We first conducted acoustic audits on the DTAG records to identify foraging buzzes, as described by Johnson et al. (2009). We then employed a supervised click detector to identify focal clicks and buzzes by determining angle of arrival, based on time difference of arrival using cross-correlation of the waveform data from the two tag hydrophones. We identified click trains from non-focal animals by their rapidly changing angle of arrival. We classified each submergence with a maximum depth of 20 m or more as a dive and identified foraging dives by the presence of at least one foraging buzz produced by the focal animal during the dive. For each dive we extracted metrics of maximum depth, duration, shape, and post-dive duration to use as potential predictors of foraging behavior. To describe dive shape we used a Wildlife Computers algorithm based on time spent at 80% of the maximum depth of the dive. We defined these metrics as follows:

$$\begin{aligned}
 D &= \text{Duration of Dive} \\
 T &= \text{Time spent at 80\% of maximum depth} \\
 V &\text{ shape if } T < 0.2 \cdot D \\
 U &\text{ shape if } 0.2 \cdot D \leq T < 0.5 \cdot D \\
 \text{Square shape} &\text{ if } T \geq 0.5 \cdot D
 \end{aligned} \tag{1}$$

For each tag deployment we determined the time of sunset and sunrise each day with the function *suncycle* in MATLAB, which uses the Naval Observatory classification system. We used these times to create a factor level for each dive as either daytime or nighttime.

We carried out all analysis using R statistical software (R Core Team 2014). We employed two different decision tree methods to assess our ability to discriminate between foraging and non-foraging dives with the DTAG data using the following predictive variables: maximum depth; duration; shape; post-dive duration; and day/night. Before running each decision tree, we split the data set into training and testing sets to assess the predictive accuracy of each method. To understand the relative contribution of each variable, we used the non-parametric Random Forest (RF) method. RFs improve statistical prediction by generating a large number of bootstrapped decision trees (based on random samples of variables) and adopting a final result by combining the results across all the trees (Liaw and Wiener 2002).

RFs are powerful classifiers, but it can be difficult to follow a single dive through the forest and arrive at the reason(s) for its classification, because there are thousands of trees and only one set of predictors (Murray and Rosauer 2011). To aid in the interpretation of the RF results and to provide applicable classification values for other researchers, we employed a Conditional Inference Tree using the function *ctree* (Hothorn et al. 2012) in the package

partykit (Hothorn and Zeileis 2014). A Conditional Inference Tree uses a significance test to select variables rather than simply selecting the variable that maximizes an information measure. This statistical approach ensures an appropriately sized tree grown and requires no pruning. We fit the models with a training dataset and determined classification error with an independent validation set.

We restricted our analysis of bouts to continuous dive records from the SLTDR tags, generated during the first 14 days of each record (one tag transmitted for only six days). We categorized dives as foraging or non-foraging based on the results of the decision tree analysis described above and conducted dive bout analysis and foraging-bout analysis for comparison. We determined Bout Ending Criteria (BEC) for each record following the methods described in Luque and Guinet (2007) using the R package DiveMove (Luque 2007). DiveMove uses maximum likelihood estimation of the distribution of the absolute difference in inter-dive duration (t), which is the time elapsed between one foraging dive and the following one. The distribution of t is assumed to be a mixture of two random Poisson processes. These processes are composed of a fast process, representing the short time scale of an individual dive, and a slow process, representing the time scale over which bouts are characterized (Sibly et al. 1990). We removed isolated dives from the analysis and included only bouts consisting of at least three dives.

3.3 Results

Individual DTAG records ranged from 1 to 18 hours in duration and the entire dataset consisted of more than 200 hours of dive records, including 330 dives and 215 foraging dives. The maximum depth of foraging dives ranged from 29 to 1,076 m. The results of the decision tree (Figure 3.3) suggested that the best predictor of foraging was the duration of a dive, with a break occurring at 400.6 seconds. The results from the Random Forest Analysis supported this conclusion, with the two most important predictors of foraging being duration and maximum depth, with shape and day/night having little predictive power. Classification error was similar in both models (Table 3.4), so we opted for the simple classification using the conditional inference tree, and thus defined a foraging dive as any submergence with a duration of more than 400.6 seconds.

We applied the predictors identified from the conditional inference tree to the six SLTDR dive records and defined 2,783 of the total of 3,572 dives as foraging dives. Mean foraging bout period across all whales was 2.18 hours, with a mean of 6.1 dives per bout and a maximum bout duration of 11.8 hours (Table 3.6). The post-dive duration varied relative to bout duration, but we identified a breakpoint at 4.53 hours in the bout duration (Figure 3.4). For foraging bouts with a duration of greater than 4.53 hours, the minimum post dive duration was 1.01 hours.

We found the mean length of dive bouts to be 3.64 hours, with an average of 13.4 dives per bout and maximum bout duration of 11.8 hours (Table 3.7). There was no discernable pattern with post-dive duration and bout duration. There was no diurnal pattern in dive behavior, nor were there any significant diel differences in the number dives per hour, foraging dives per hour, or average maximum depth of foraging dives (Table 3.8).

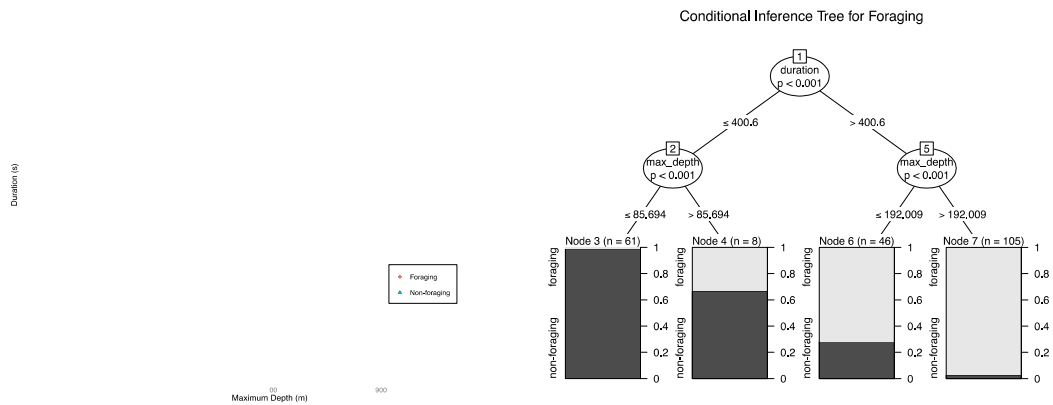


Figure 3.3. Results of DTAG analysis. The pane at left is a plot of maximum depth vs. duration with red circles representing non-foraging dives and black circles representing foraging dives. The pane at right is a classification tree produced by analysis of predictors of foraging dives. Bar plots in the non-branching nodes indicate the relative dropouts with particular combinations of relative predictors.

Table 3.2. Confusion matrix for Random Forest Analysis

	Reference	
Prediction	aging	52

Table 3.3. Confusion matrix for Conditional Inference Tree

	Prediction	
Reference	ging	51

Table 3.4. Comparison of overall accuracy and statistics between the two classification methods

Test Statistics			
95% CI			

Table 3.5. Variable importance determined in Random Forest Analysis. The mean decrease accuracy reflects the reduction in accuracy if the variable was removed from a decision tree.

Variable	Importance	Mean decrease accuracy
3.6	26.4	

Table 3.6 Foraging bout analysis

Animal ID	ls

Table 3.7. Dive bout analysis

Animal ID							

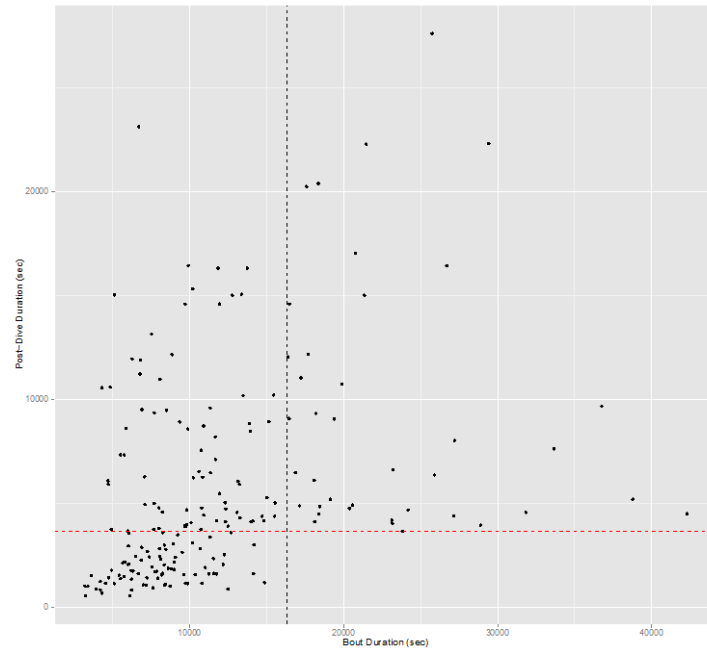


Figure 3.4. Surface durations following foraging bouts. The black dashed line represents a breakpoint in bout durations (4.53 hours). The red dashed line represents minimum surface duration following the break (1.01 hours)

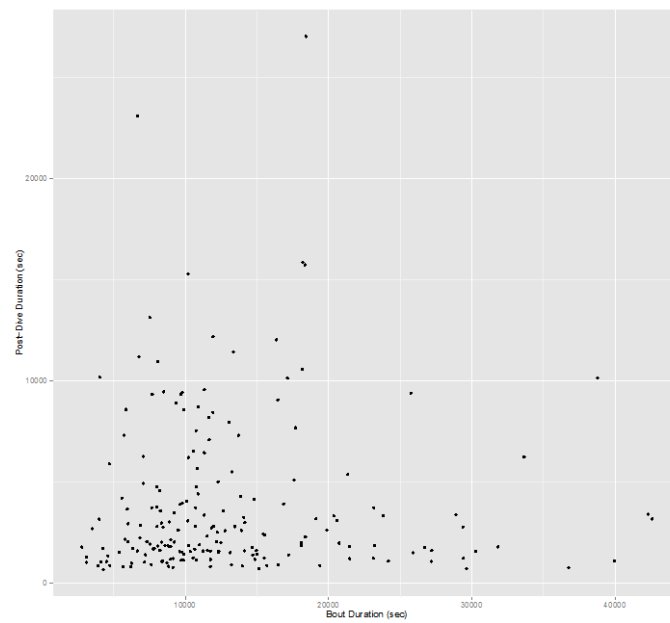


Figure 3.5. Surface durations following dive bouts

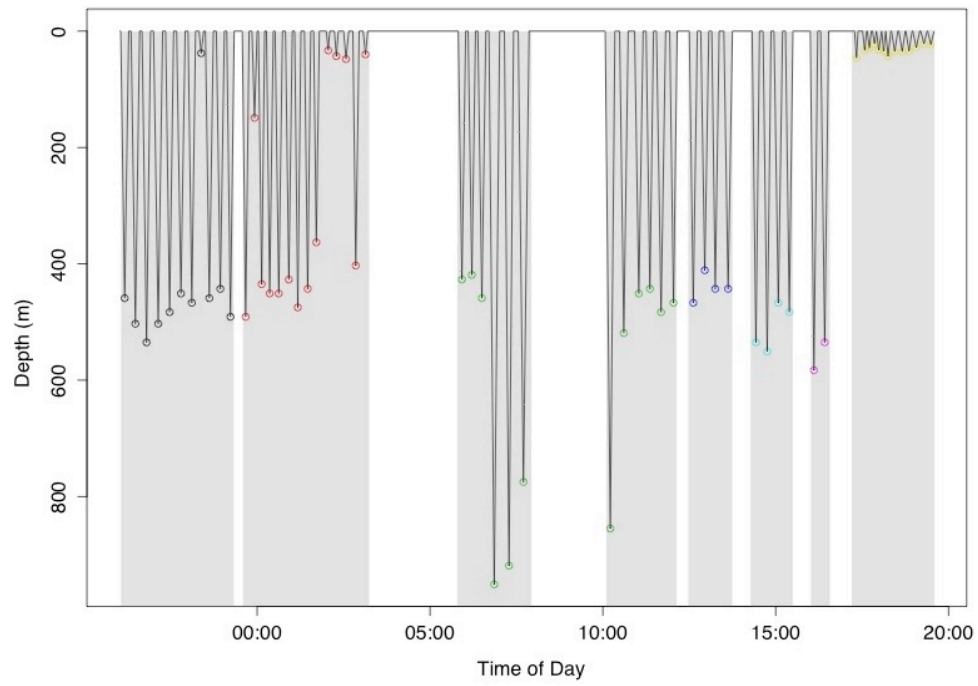


Figure 3.6. Dive record of pilot whale GmTag085 with bouts highlighted by shading

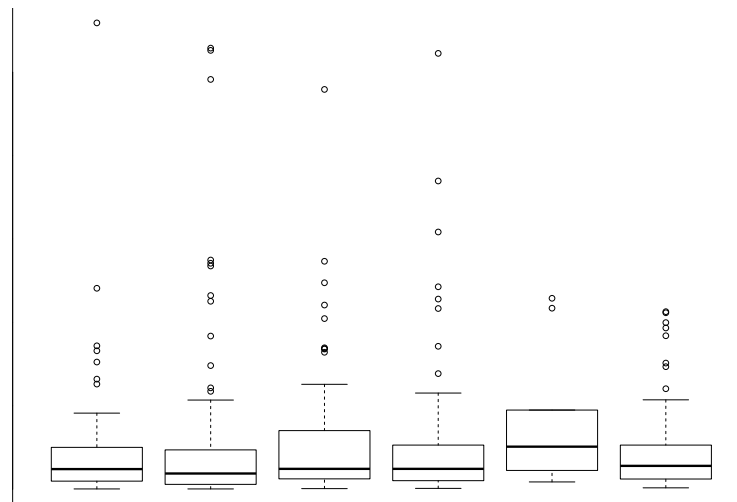


Figure 3.7. Bout durations for each SLTDR deployment

Table 3.8. Diel variation in foraging rates, dive rates, and average depths

Animal ID

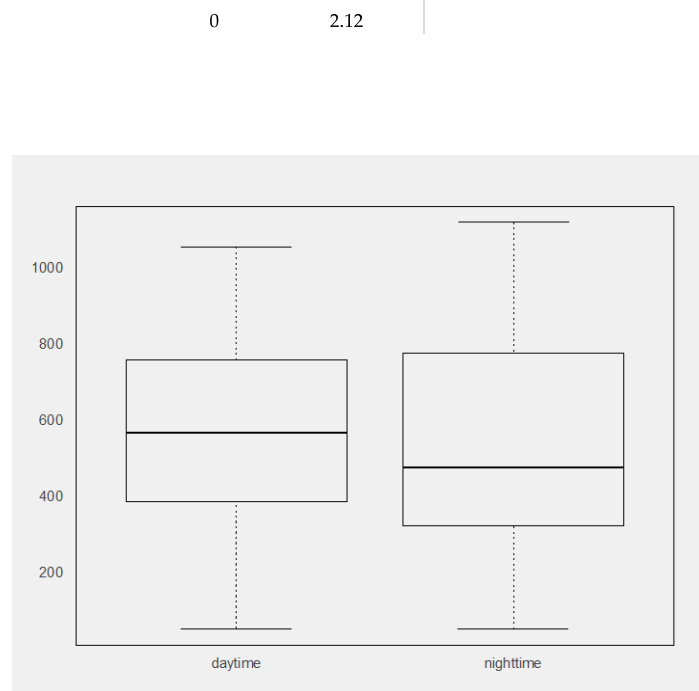


Figure 3.8. Box and whisker plot of depth of foraging dives during day and night.

3.4 Discussion

The multi-scale approach we employed here provided insight into pattern and variation of the foraging behavior of short finned pilot whales off Cape Hatteras. Studies of pinnipeds have used high-resolution data to assist in the classification of sub-surface behavior (Austin et al. 2006; Gallon et al. 2013; Viviant et al. 2014), but this is the first study, to our knowledge, to attempt such validation with cetaceans. In addition, this baseline data provides a strong basis for subsequent analysis of behavioral response studies, in large part because it represents one of the largest such data sets for any cetacean species.

We found that dive duration was an excellent predictor of foraging behavior in short-finned pilot whales, with a classification error of only 6%, similar to or better than other studies of dive classification (Austin et al. 2006; Viviant et al. 2014). Other traditional metrics, such as dive shape, are poor predictors of foraging behavior in pilot whales. BEC varied across animals, but the duration of foraging bouts and the number of dives in a foraging bout were fairly consistent. Foraging bouts longer than 4.5 hours required at least an hour of recovery time at the surface. Maximum durations of foraging and dive bouts were similar, but dive

bouts were, on average, longer than foraging bouts. There was no discernable pattern in surface durations following dive bouts.

Other studies of marine mammals have employed dive duration as an indicator of foraging behavior (Austin et al. 2006; Baechler et al. 2002; Costa and Gales 2000; Lesage et al. 1999). We expect diving vertebrates to engage in foraging tactics that respond to the availability and quality of prey species (Bowen et al. 2002). Thus, diving whales should lengthen their dives when they encounter a profitable prey patch. Optimal foraging theory predicts that animals should behave in a way that will maximize their net energy gain and, when it is profitable, diving mammals may exceed their aerobic limits to maximize foraging time (Costa et al. 2004; Hazen et al. 2015). It is unclear why some of the other dive metrics, particularly dive shape, are less useful in predicting foraging behavior. At least some of the pilot whales were foraging near the sea floor and it is possible that variation in depth and topography along the shelf break led to complex dive shapes that precluded simple classification.

Overall, the pilot whales we studied demonstrated considerable variation in foraging behavior. The whales made foraging dives from 29-1215 meters and that lasted from 6.5 to 26 minutes. This range of depth and duration implies considerable plasticity in foraging strategies, and perhaps a mixture of foraging and non-foraging behavior, and supports the hypothesis that this species forages on a range of species off Cape Hatteras.

Foraging performance is ultimately constrained by physiological limits, including digestive capacity, gas management and thermal balance (Costa et al. 2004; Hooker et al. 2009; Rosen et al. 2007). These limits are likely reflected in the maximum observed duration of foraging bouts, which ranged from 8.8 to 11.8 hours for individual whales (Table 3.4). In addition, it appears that whales must undertake periods of rest after long foraging bouts (Figure 3.4). We do not yet understand what factor or factors ultimately limit the duration of foraging bouts in this species. This will require further study of pilot whale diving physiology and digestive capacity, as well a more complete understanding of the distribution and availability of their prey.

Surprisingly, we observed no diel patterns in foraging rates or depth on DTAG or SLTDR records, contradicting our predictions based on observed prey in the stomachs of stranded pilot whales off Cape Hatteras (Mintzer et al. 2008) and from observations of the foraging behavior of other odontocete cetaceans (Baird et al. 2002). We remain puzzled that pilot whales do not take advantage of diel variation in the availability of potential prey items in the DSL. The decisions made by foraging pilot whales are complex and may involve tradeoffs between energy expenditure and return that are difficult to elucidate without direct measurements of the availability of prey at various depths. Nevertheless, our observations do not preclude the possibility that pilot whales forage in the deep scattering layer. In fact, the relatively large variance in nocturnal foraging depths would seem to imply that they do, on occasion, take advantage of this resource.

It is difficult to compare our results with those of pilot whales elsewhere because there are so few published observations of the foraging behavior of this species. In the only other large-scale published study, Soto et al. (2008) used DTAGs to study the foraging behavior of 23 short-finned pilot whales off Tenerife, in the Canary Islands. At a coarse level, their observations were similar to ours, with foraging dives reaching depths of 1,018 m and lasting up to 21 minutes. These authors focused their attention on a subset of foraging dives during daylight hours, in which tagged animals made downward directed sprints, presumably in

pursuit of large prey items. Soto et al. (2008) reported some apparent diel variation in foraging behavior, with deeper dives made during daylight hours, but with fewer foraging buzzes than foraging dives made at night. Given the high level of variation observed in other aspects of the behavior of this species, we predict that differences in foraging strategies among populations of short-finned pilot may reflect variation in the environment and prey fields.

The definition of foraging bouts, as described here, has important implications for our understanding of the effects of disturbance on this species. In many mammals, cessation of foraging is considered to be an important response to anthropogenic disturbances, because it has obvious consequences for the fitness of the individual (Southall et al. 2008). Our study will benefit future behavioral response studies with short-finned pilot whales, because we can now predict the probability that an animal will stop foraging in an undisturbed state. We can then use this baseline information to compare with observed changes in behavioral state to determine the probability that a cessation in foraging was caused by a particular stimulus. Few prior studies have attempted to analyze the foraging bouts of cetaceans because of limited data records (particularly with DTAGs) or difficulties in defining foraging dives. Our multi-scale approach has overcome the limitation of previous data records by combining long (14 day) and short (one day) records for individual whales monitored by SLTDRs and DTAGs, respectively. In addition, we have developed a simple and systematic method of using dive metrics generated from DTAG data to distinguish foraging from non-foraging dives in long-term SLTDR records.

Chapter 4: Hidden Markov Models reveal complexity in the diving behavior of short-finned pilot whales

4.1 Introduction

Cetaceans live the vast majority of their lives underwater and engage in a great variety of sub-surface behavior. Classification of any repertoire of diving behavior requires identification of objective criteria that allow an observer to discriminate various dive types; several methods have been used to identify such categories (see Hooker and Baird 2001 for a review). These range from subjective grouping of dives based on certain characteristics (e.g. maximum depth) to the objective use of statistical techniques. Analysis of diving behavior in cetaceans has been improved by the development of animal-borne tags that provide high resolution data on kinematic and acoustic behavior (Johnson et al. 2009). However, analyzing complex time series data and quantifying the likelihood of individual behavior based on a series of observed data points from a tag record presents a particular set of challenges. Inherent differences among individual animals, motivational states and environmental factors may all contribute to observed behavior. Furthermore, it is difficult to scale up from an individual tag record to a population-level behavioral model.

The use of non-invasive digital acoustic recording tags (DTAGs), attached via suction cups (Johnson and Tyack 2003) has provided detailed records of diving behavior in a number of deep-diving cetaceans, including sperm whales *Physeter macrocephalus* (Miller et al. 2004), beaked whales (Johnson et al. 2004; Stimpert et al. 2014; Tyack et al. 2006), short-finned pilot whales *Globicephala macrorhynchus* (Soto et al. 2008; Jensen et al. 2011) and long-finned pilot whales *Globicephala melas* (Sivle et al. 2012; Visser et al. 2014). DTAGs provide kinematic and depth measurements of sub-surface behavior, together with a synchronized acoustic record, providing a rich set series of variables that can be associated with diving behavior.

Pilot whales are highly social odontocetes found world-wide in waters of the shelf break and slope (Olsen 2009). Two species exist and both, long-finned and short-finned pilot whales, are deep divers capable of performing foraging dives to many hundreds of meters. (Alves et al. 2013a; Baird et al. 2002; Heide-Jørgensen et al. 2002; Jensen et al. 2011; Nawojchik et al. 2003; Soto et al. 2008; Wells et al. 2013). Despite a basic knowledge of their deep diving capacity, definition of diving behavior in pilot whales is generally limited to two broad categories; deep foraging dives, and all other (generally shallower, non-foraging) dives. Temporal clustering or bouts of dives has been suggested for long-finned pilot whales, with periods of shallow diving followed by bouts of deep diving (Sivle et al. 2012; Visser et al. 2014). For short-finned pilot whales, dive records are suggestive of temporal clustering, but no information exists about transitions between diving states.

Four previous studies deployed DTAGs on pilot whales and, in each case, diving behavior has been defined primarily by depth of submergence. For short-finned pilot whales, Jensen et al. (2011) defined deep dives as those exceeding 300 m. Soto et al. (2008) initially scored a dive as any submergence of more than 20 m and then discriminated between shallow and deep dives using a second threshold of 500 m. For long-finned pilot whales, Sivle et al. (2012) and Visser et al. (2014) used a log frequency analysis to define a cut-off value of 34 m to separate shallow and deep dives. Dives were then classified as foraging dives by the presence of vocal behavior (click trains and buzzes), similar to those seen during in other

deep diving odontocete cetaceans, such as beaked and sperm whales (Johnson et al. 2004; Miller et al. 2004), and short-finned pilot whales (Soto et al. 2008). Diving behavior in pilot whales may approximate an optimal solution to the trade-off of maximizing foraging time versus available oxygen stores, as has been suggested for other diving vertebrates (Mori 1998; Stephens et al. 2008). However, Soto et al. (2008) demonstrated a high-risk, high-gain strategy employed by short-finned pilot whales off Tenerife, in which whales engaged in daytime foraging dives to target large, high-value, fast moving prey. These observations are in contrast to the predictions of optimal foraging theories of maximizing time at depth based on the scaling relationship between mass and metabolic rate, and more in line with suggestions that prey quality may shape foraging strategies (Spitz et al. 2012). However, stomach contents of mass-stranded pilot whales off Cape Hatteras, North Carolina revealed a diet of small-bodied mesopelagic squid (Mintzer et al. 2008), suggesting that foraging strategies may differ among populations of this species. Furthermore, the existence, albeit rare, of foraging buzzes during relatively shallow dives (Soto et al. 2008) suggests that diving behavior in short-finned pilot whales may be more complex than a simple dichotomy of deep foraging and shallow, non-foraging diving states.

In the present study we use multi-state hidden Markov models (HMMs) to classify hidden Markov states in short-finned pilot whales, based on DTAG data. The HMM allows us to classify dives objectively into the most likely state sequence given our observations. We use three observed variables for each dive that we consider predictors of dive type, to objectively assign the state and the transitions between them. We modeled the three observed dive variables as independent, conditional on the sequence of hidden states (Altman 2007; Langrock et al. 2012) within multi-state models.

4.2 Materials and Methods

We equipped 20 short-finned pilot whales off Cape Hatteras, North Carolina, with Version 2 DTAGs (Johnson and Tyack 2003) between 2008 and 2014. This is a sub-set of the DTAG deployments described above in Chapter 3 – it differs by not including any of the baseline periods for whales that were the subject of playback experiments. We tagged whales from a variety of small Rigid-Hull Inflatable vessels (all less than 10-m) in variable sea states (Beaufort 0-4), using a carbon-fiber pole to attach the tag to the dorsal surface or fin of the whale. The DTAG is a multi-sensor tag, attached via suction cups that records: audio with 16-bit resolution at a sampling rate of 96 – 192 kHz; depth at 50 Hz; and orientation of the whale from tri-axial accelerometers and magnetometers at 50Hz (Johnson and Tyack 2003). We programmed the tags to release after a predetermined period, if they had not already detached from the animal, we located them using a VHF radio transmitter embedded in the tag.

In general, we selected a well-marked, large animal in a discrete group as the animal for tagging. Prior to tagging, we obtained photographs of the dorsal fins of all individuals within the group for identification purposes. We avoided groups containing neonates. After tagging, we conducted focal follows of the tagged animal and its group, employing point sampling every five minutes. The focal group was defined as all individuals within 30 m (approximately 10 body lengths) of the focal individual. Information on group size, group spread, synchrony of surfacing, heading synchrony, behavioral state and activity level for each state were recorded. We also recorded range and bearing of the focal animal from the follow boat. Focal follows continued for the entire duration the tag was on the animal, unless

periods of poor visibility rendered following impossible, or if animals were temporarily lost from view. We obtained biopsy samples from eleven of the whales (typically immediately following release of the DTAG) and determined sex for nine of these individuals (Table 4.1). A quantitative analysis of tagging effects on short-finned pilot whales off Cape Hatteras showed no evidence of disruption of foraging behavior and only low intensity responses to biopsy sampling (Crain et al. 2014).

We downloaded data from the tags and converted pressure recordings to depths using calibration information for each tag (Johnson and Tyack 2003). We also performed calibration of the orientation offset from tag position and down-sampled all movement data to 5 Hz. We defined a *dive* as any submergence to a depth of 20m or deeper. Any interval of data recorded at a depth of 20m or less was considered time spent at the surface. We calculated three dive parameters for each dive: *Dive duration*, the time between the start of descent and the end of ascent (minutes); *Maximum depth*, the maximum depth reached during dive (meters); *Number of buzzes*, the number of echolocation buzzes recorded during the dive duration. Each parameter was calculated over the period of a single dive (from time at surface when the dive began to the time when animal returned to the surface). We disregarded incomplete data from any dive in which the tag was jettisoned. All acoustic audits of the DTAG sound files, to determine time of buzzes, indicative of foraging attempts (Soto et al. 2008; Jensen et al. 2011), were conducted by a single experienced analyst.

We used a multivariate mixed Hidden Markov Model (HMM) as a framework for the analysis. The model was a first-order Markov model and assumed that the distribution of the current state is determined only by the previous state (Rabiner 1989; Zucchini and MacDonald 2009). The three dive and movement variables from each dive were specified as the observable series and each dive was assigned to the individual whale in the order that it occurred. Three models were constructed based on two, three and four underlying non-observable behavioral states and that the observations were conditionally independent given the states, i.e., contemporaneous conditional independence was assumed (Zucchini and MacDonald 2009). We assumed that the states are interconnected and that any hidden Markov state could be reached from any other hidden Markov state. We included all dives from all individuals in the models. We did not consider individual random effects in the models, and assumed all whales shared common distribution parameters for all variables (Langrock et al. 2012).

We fitted the models via numerical maximum likelihood estimation using the *nlm* optimiser in R (R Core Team 2014; see Zucchini and MacDonald 2009 for details of implementation). To improve confidence that the global minimum was found during the maximization process, we specified 100000 initial values and investigated the likelihood surface prior to maximization. This enabled only those values with the highest likelihoods to be passed to the *nlm* optimiser for maximization. One hundred simulation runs of the model were completed to check for numerical stability in robustness against different initial values in the minus log likelihood. We applied the Viterbi algorithm (Forney 1973) to each individual animal and used it to find the most likely sequence of hidden states given the observed variables and the transition probabilities between states.

Table 4.1. Summary of tagging information, including the number of dives assigned to each state. Tag ID is based on the Julian day with the letter representing the sequential order in which the animal was tagged (a= first animal tagged that day, b = second and so forth). Biopsy, Y is a biopsy obtained, N is no biopsy obtained. Sex was obtained from the biopsy data, M= male, F=female, U= unknown (sample not processed), - = no biopsy taken. Total dives indicates the number of dives used in the analysis. Number of dives per state shows the allocation of dives from the HMM.

Date	Tag ID	Time on (local)	Time off (local)	Total Time (hh:mm)	Biopsy	Sex	Total dives	#dives per state			
								1	2	3	4
22-May-08	143a	14:28	17:42	03:14	N	-	4	2	2	0	0
22-May-08	143b	18:18	22:49	04:31	N	-	9	3	0	6	0
26-May-08	147a	15:02	17:20	02:18	N	-	7	7	0	0	0
30-May-08	151a	08:46	10:17	01:31	N	-	3	1	1	1	0
30-May-08	151b	13:14	06:32	17:18	N	-	17	9	1	7	0
04-Jul-10	185b	14:30	20:20	05:50	Y	F	5	1	3	1	0
05-Jul-10	186a	11:10	11:40	00:30	N	-	2	2	0	0	0
05-Jul-10	186b	14:32	20:03	05:31	Y	F	3	3	0	0	0
06-Jul-10	187b	12:53	06:15	17:22	Y	M	34	2	18	13	1
27-Jul-10	208a	14:50	23:47	08:57	Y	F	34	9	0	25	0
28-Jul-10	209a	08:54	10:12	01:12	Y	M	3	0	1	2	0
28-Jul-10	209c	13:19	20:09	06:50	Y	M	4	1	0	3	0
23-Sep-10	266a	18:35	12:49	18:14	N	-	32	3	11	4	14
24-Sep-10	267a	15:19	09:19	18:00	Y	M	64	7	1	43	13
29-May-11	149b	10:33	14:24	03:50	Y	M	7	1	6	0	0
30-May-11	150b	11:11	14:46	03:34	N	-	7	2	4	1	0
05-Jun-11	156a	12:11	16:29	04:17	N	-	3	0	0	3	0
14-Jun-11	165a	09:25	13:43	04:17	Y	M	9	0	7	2	0
07-Oct-14	279a	12:42	16:09	03:27	Y	U	10	5	2	0	3
08-Oct-14	280a	12:31	15:12	02:41	Y	U	2	1	0	1	0

4.3 Results

The 20 deployments produced 133 hours and 24 minutes of tag time (Table 4.1). The DTAGs were deployed for periods that varied from 0.5 to more than 18 hours (median 4 hours, 17 minutes) and the number of dives per individual ranged from 2 to 64 (Table 4.1). Tag data were not distributed evenly through day and night hours, as we attached all tags during daylight hours. Eleven of the tags recorded only during daylight hours, with tag off times prior to 18:00 hours. Three other tags released prior to 20:30 during summer months, when daylight was reduced. A further two DTAGs released after 22:30 but prior to midnight and four tags remained on overnight, releasing after 06:00 the following morning (Table 4.1). We determined sex for nine individuals, including three females and six males (Table 4.1).

The four state hidden Markov model (HMM) consistently produced better AIC (four-state, 2332.077; three-state, 2559.844; two-state, 3104.718) scores than the two or three state models. Re-running all models showed stable AIC scores and minus log-likelihood scores, and consistent state allocation of all dives across all individuals. We consider the four states to represent different types of dives in short-finned pilot whales. State 1 included shallow dives, characterized by short durations and no foraging buzzes. State 4 dives were of greater depth, longer duration with a high buzz rate. States 2 and state 3 were intermediate between state 1 and state 4 dives, with state 3 dives being shallower, shorter and with fewer buzzes than state 2 dives (Table 4.2, Figure 4.1).

Table 4.2. State summaries of observed variables for each state

State	Variable	Mean	Median	Min	Max
1	Dive Duration (mins)	4.02	3.6	1	9.61
2	Dive Duration (mins)	13.81	13.77	10.42	18.15
3	Dive Duration (mins)	10.23	9.88	4.55	17
4	Dive Duration (mins)	18.55	18.27	15.8	22.52
1	Max Depth (m)	43	34	20	128
2	Max Depth (m)	562.09	535	245	826
3	Max Depth (m)	213.86	193	30	587
4	Max Depth (m)	843.1	848	578	1052
1	Number of Buzzes	0.07	0	0	1
2	Number of Buzzes	11.65	11	3	29
3	Number of Buzzes	3.28	3	0	15
4	Number of Buzzes	30.45	29	17	54

Analysis of each dive by variable (Figure 4.2) showed overlap between the four states and variation between dives within each state (Figure 4.2 and Figure 4.3). Overlap in variable range was seen between many of the states (Table 4.2 and Figure 4.3), particularly states 2 and 3, which overlapped considerably for each variable. State 1 had the narrowest range for

two variables (Figure 4.3) and never overlapped with state 4 for any variable. The observed overlap was generally driven by a few outlying dives in each state. For example, in state 1 all but four dives contained no buzzes (Figure 4.2) and dives were generally shallow (mean depth 43m) and of short duration (mean 4.02 minutes). The four dives in State 1 that contained buzzes had maximum depths of 60, 60, 74 and 87 m and durations of 3.6, 5.6, 1.8 and 5.7 minutes, comparable in depth and duration to all other dives in the state. For state 2, the shallowest dive (245m) had a dive duration (12.8 mins) and number of buzzes (9) that were just below average. In state 3, two dives of long duration (15 mins, state mean is 10.15 mins) and average and high buzz number (3 and 8 buzzes, mean buzzes is 3.28) were the shallowest in the state, both less than 40 m deep (state 3 mean depth was 213.86 m, Table 4.2). For state 4, the shallowest dives in the state had longer than average durations and an average number of buzzes for the state (Table 4.2, Figure 4.2).

The proportion of dives within each state was not equal. Fifty-nine of the dives across 17 individuals were allocated to state 1; 57 dives across 12 individuals to state 2; 112 dives across 14 individuals to state 3 and 31 dives across four individuals to state 4 (Table 4.1, Figure 4.4). Only four individuals displayed only a single type of dive state; eight displayed two types of dive state; five displayed three types of dive state and three displayed four types of dive state (Figure 4.4). All four diving states were seen during both day and night (Figure 4.5). None of the three female whales displayed any state 4 dives (Table 4.1), but they displayed all other dive types. The six known male animals displayed all dive types, with two showing state 4 dives.

State persistence and state switching was observed within and across all states. The transition probabilities between states were all considerably higher for state persistence than state switching for all states, indicating that same-state dives occur in bouts (Table 4.3, Figure 4.5). The highest transition probabilities were seen for persistence in states 2 and 3 and the lowest in state switching between state 3 to state 4 and state 1 to state 4 (Table 4.3). Mapping probability of state onto the dive profiles supported the existence of bouts, *i.e.* state persistence, but also showed examples of state switching (Figure 4.5).

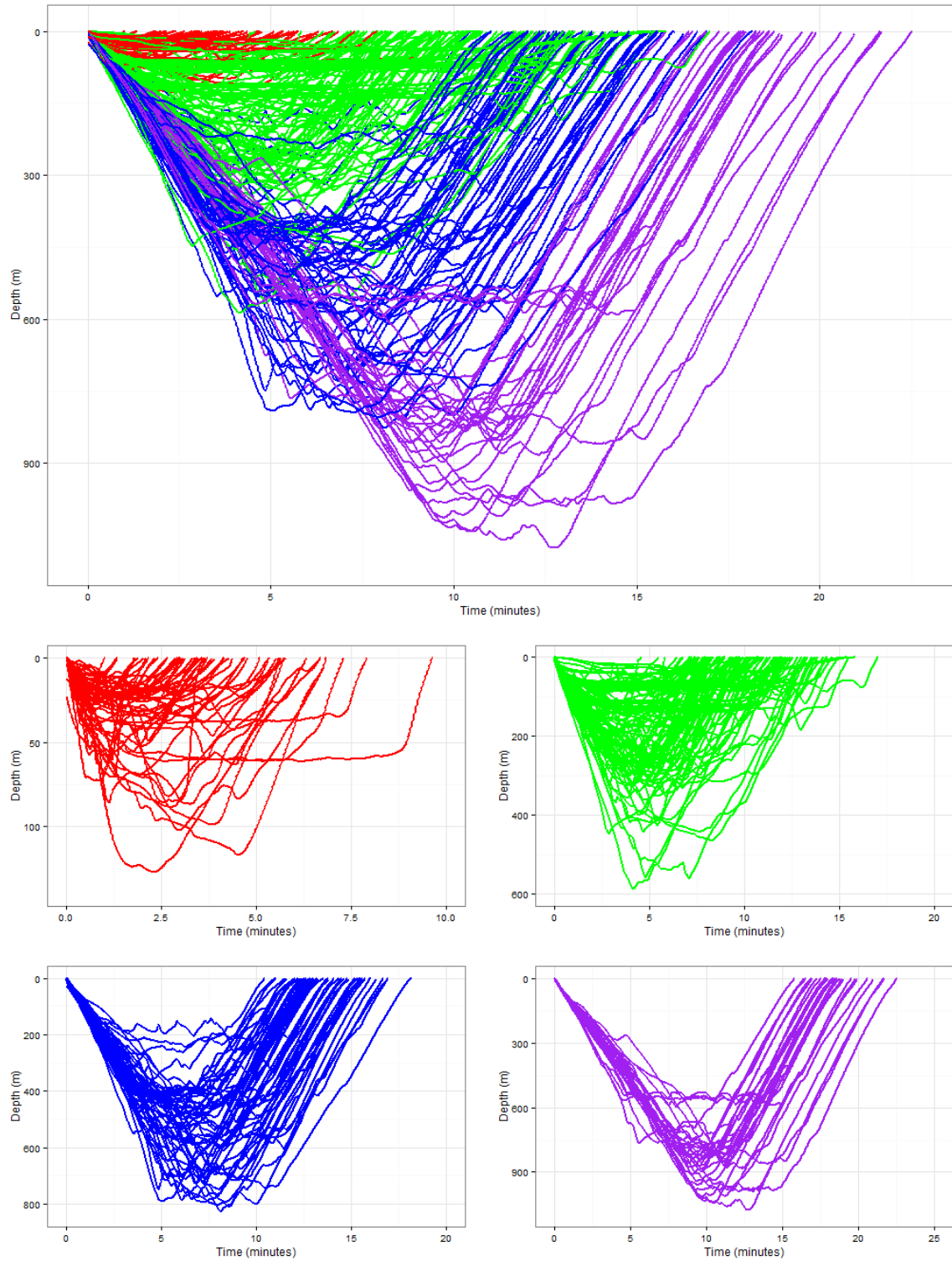


Figure 4.1. Dive allocation per state for all dives from all individuals. Red = state 1, blue = state 2, green = state 3, purple = state 4. Top panel shows all dives from all states. Bottom four panels show each state individually. Note different x and y axis scale.

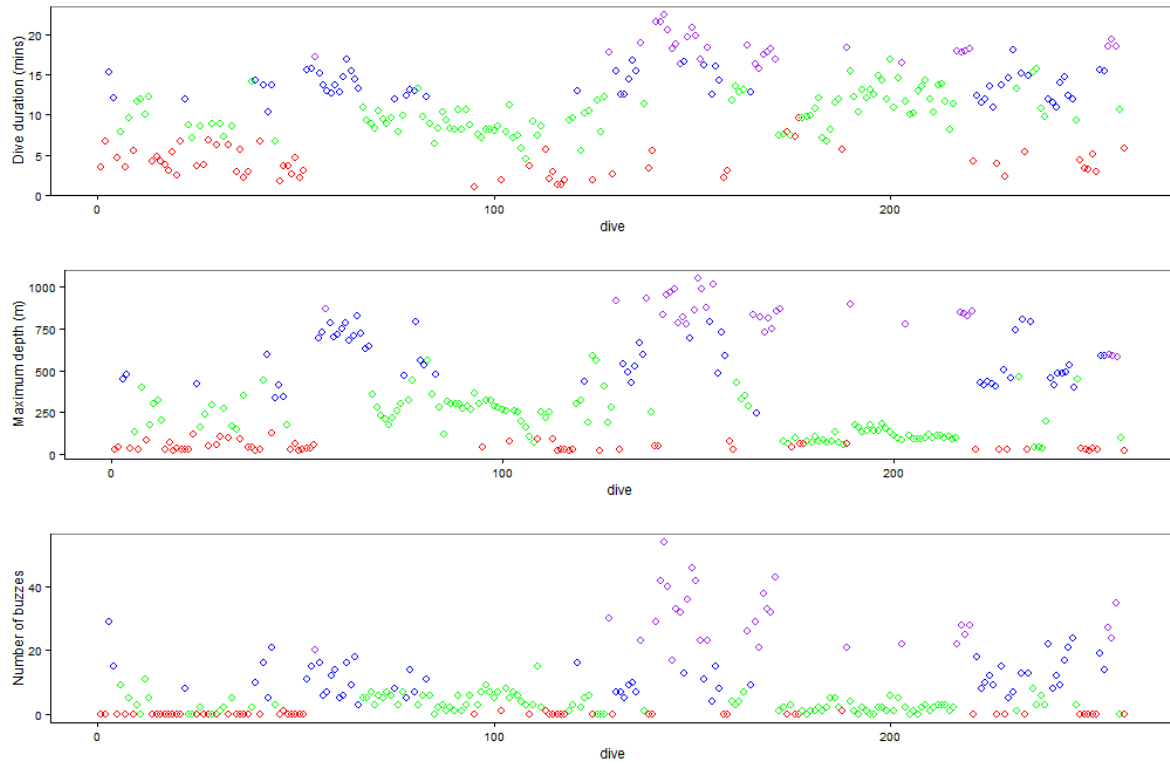


Figure 4.2. State allocation per dive for each of the three observed variables. Red represents state 1; blue represents state 2; green represents state 3 and purple represents state 4.

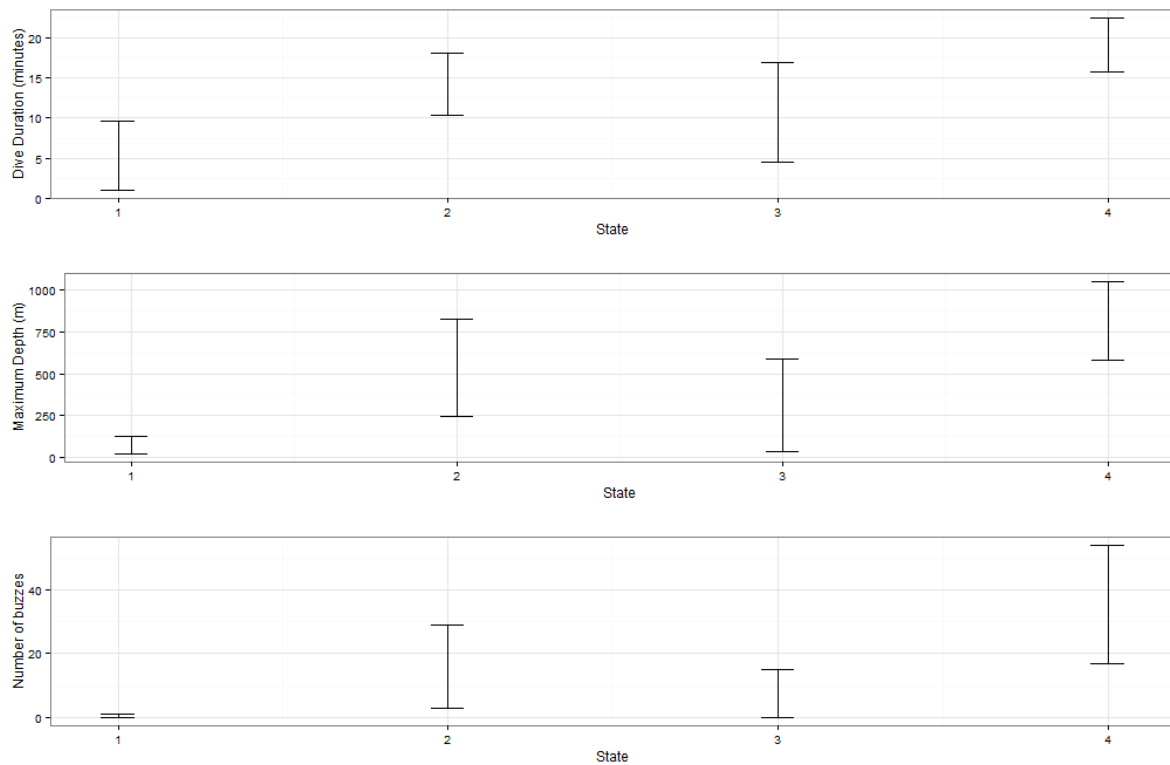


Figure 4.3. Range overlap (min-max) for each of the three variables for all four states.

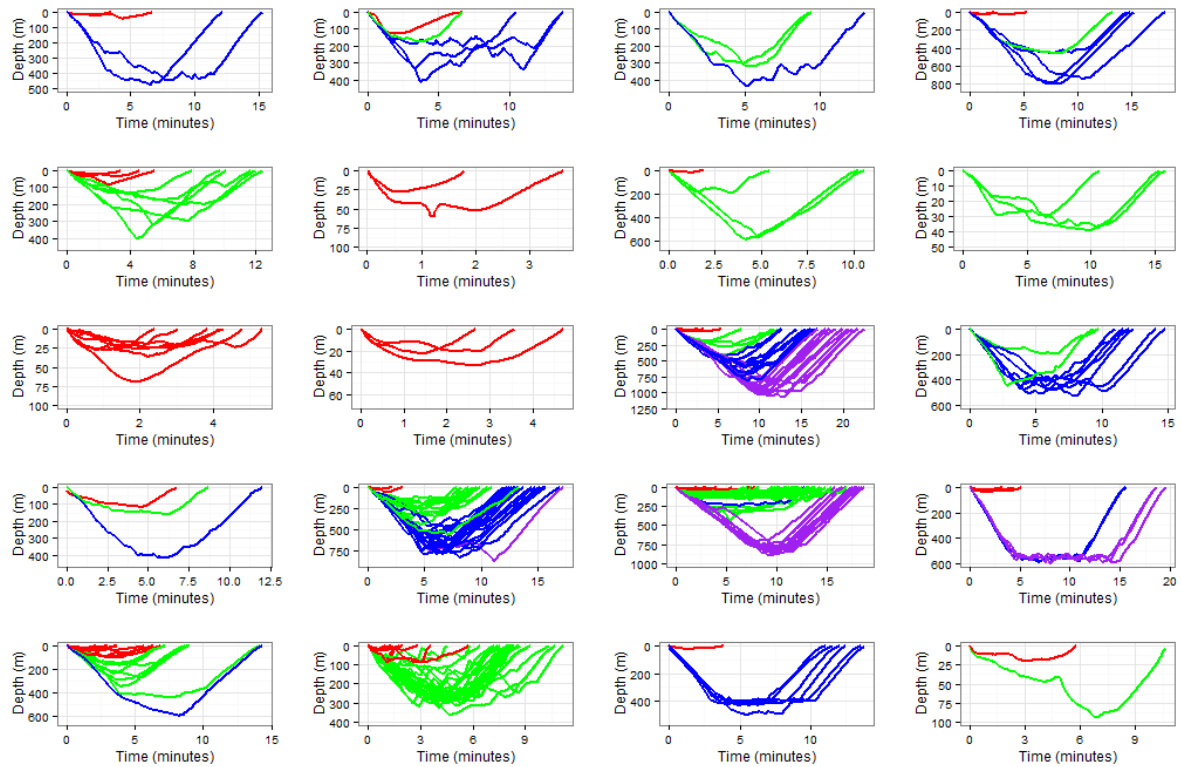


Figure 4.4. Dive allocation per individual. Red = state 1, blue = state 2, green = state 3, purple = state 4. See Table 4.1 for individual information; First column, individuals 143a-151b; second column, individuals 185b-208a; third column, individuals 209a-149b; fourth column, individuals 150b-280a. Note different x and y axis scales.

Table 4.3. Transition probabilities for both states and number of dives within each state

	State 1	State 2	State 3	State 4	Number of dives
State 1	0.526	0.168	0.275	0.030	59
State 2	0.040	0.714	0.134	0.112	57
State 3	0.142	0.087	0.730	0.041	112
State 4	0.069	0.148	0.140	0.643	31

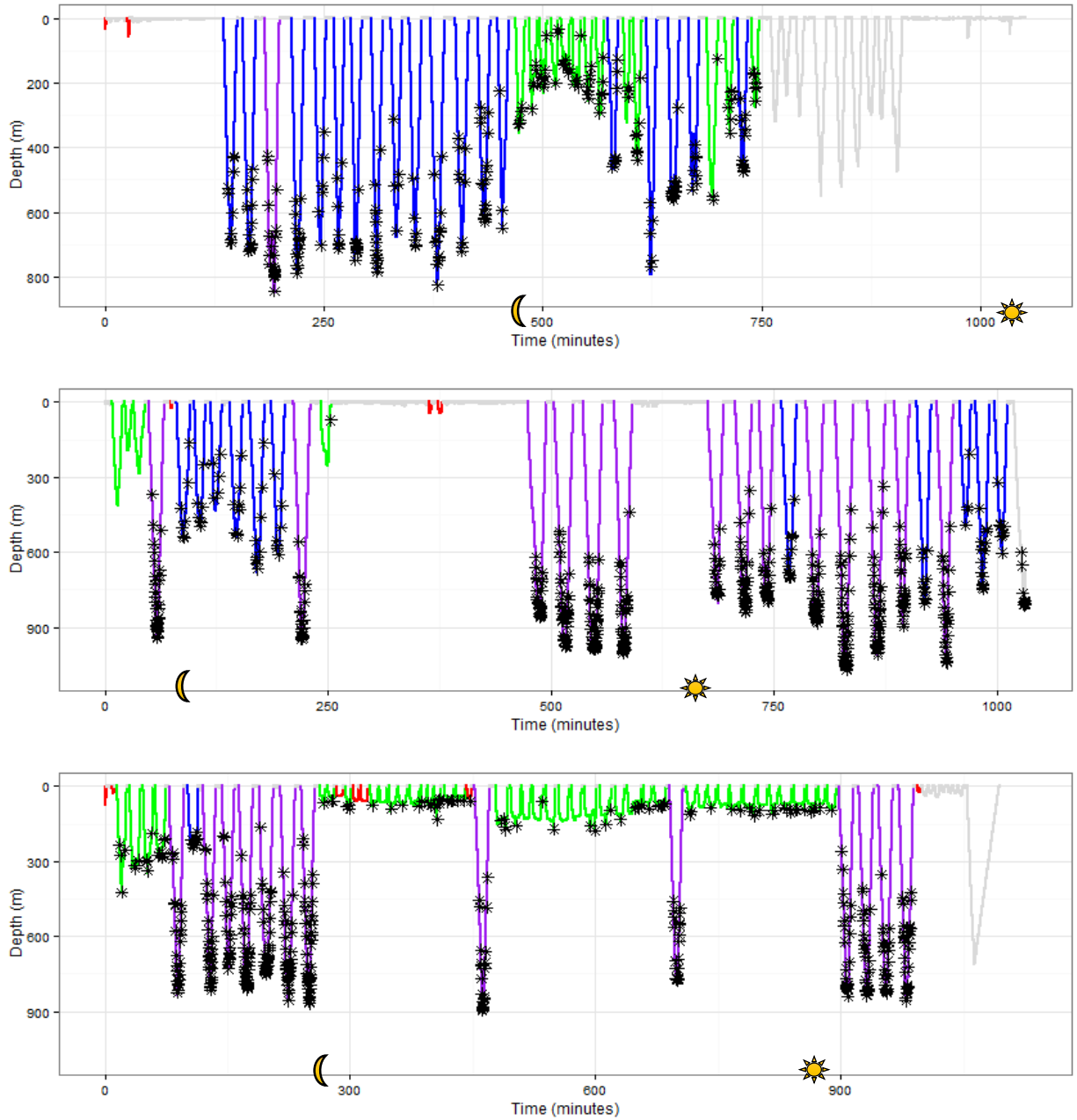


Figure 4.5. Dive profile data from three individual pilot whales (top: Gm10_187b, middle: Gm10_266a, bottom: Gm10_267a) with the probability of state mapped onto the dives. Red lines indicate highest probability of being in state 1, blue lines indicate highest probability of being in state 2, green lines indicates highest probability of being in state 3 and purple lines highest probability of being in state 4. Grey lines indicate data not used in the analysis, this includes information classified as at the surface, incomplete dives or dives lacking acoustic records. Black asterisks identify individual buzzes, yellow moon on x axis indicates approximate time of sunset (20:00) and yellow sun indicates approximate time of sunrise (6:00). Note different x and y axis ranges.

4.4 Discussion

Our findings indicate that the diving behavior of short-finned pilot whales is much more complex than a simple dichotomy of deep and shallow diving states and, furthermore, that there is considerable variability in diving behavior across individuals. The HMM identified four states observed across multiple individuals and provided insight into patterns of state persistence and state switching. Our predictions of state are based on the distribution of three readily observed variables. We chose dive duration, maximum depth and number of buzzes as good descriptors of diving behavior based on previous studies of diving behavior in this species (Alves et al. 2013a; Soto et al. 2008; Jensen et al. 2011). Most prior studies of this species have used depth alone to define two states (deep and shallow) of dives. Furthermore, as noted by Alves et al. (2013a), various depths have been used to differentiate shallow non-foraging and deep foraging dives in pilot whales (Baird et al. 2002; Soto et al. 2008; Jensen et al. 2011; Sivle et al. 2012; Visser et al. 2014). The HMM allows us to classify diving behavior objectively using relevant observational variables, whilst accounting for the autocorrelation in the time series data and computing the most likely state sequence and the transitions between states.

We consider State 1 to be a shallow, non-foraging diving state, State 2 as an intermediate deep foraging state, State 3 as an intermediate shallow (or perhaps less successful) foraging state and State 4 as a deep foraging state. All four states showed temporal clustering, indicating that these states occur in bouts, but not all individuals displayed all states. This is likely due, at least in part, to the variation in total tag retention time across individuals, as animals tagged for a shorter time displayed fewer diving states than those tagged for longer periods. State persistence, for all states, was shown by some individuals for more than 200 minutes, indicating that shorter duration tags may provide only a snap-shot of diving behavior. The five whales monitored for the shortest periods (less than 3 hours, Table 4.1) displayed only one or two states, in contrast to the six animals tagged for the longest periods (greater than 6 hours, Table 4.1) which exhibited either two, three or four diving states. There are no published studies of time activity budgets of short-finned pilot whales, but studies from other highly social cetacean species demonstrate that individuals often engage in bouts of behavior and rarely behave in a sequentially random fashion (Karniski et al. 2015). It is, therefore, possible that the longer the monitoring period, the higher the probability of recording all diving states, if all individuals are equally likely to engage in all states. However, it is difficult to predict whether every individual will engage in all four states without understanding the mechanisms that drive the differences among states and determining which specific behavior is represented by each state.

State 1 was characterized by dives of shallow depth, short durations and, for all but four dives, the absence of foraging attempts (buzzes). The mean depth value (43m) was similar to the cut-off value used for defining shallow and deep diving states in long-finned pilot whales (Sivle et al. 2012; Visser et al. 2014). We consider this state to represent non-foraging behavior, but we are unable to conclude a specific function for this state from our data, and suggest only that these dives could serve a social or kinetic function. State 1 dives were seen across multiple individuals, with a higher probability of state persistence than state transition, suggesting they represent a defined, rather than random, behavior or group of behaviors. Short finned pilot whales are highly vocal animals (Sayigh et al. 2013), and rely on acoustic communication to maintain social bonds. The increased propagation of sound underwater compared to in air (Richardson et al. 1995)

suggests that pathways for acoustic communication are maximised below the surface. Similarly, a reduction in surface drag to aid efficient movement (see Williams 2009 for a review) suggests more efficient locomotion could be performed sub-surface. State 1 dives could, therefore, represent either (or both) of these behaviors. However, further investigation using observations that are descriptors of non-foraging behaviors, such as social call rates, or speed of movement, is required to further understand the function of State one dives.

We consider State 2-4 dives to represent foraging behavior, due to the presence of foraging buzzes, greater maximum depths and longer dive durations. However, this group of States include considerable variation in mean values for all variables and there may be a number of plausible explanations driving the different diving behavior, including physiological limitations, prey selection and abundance, geographic topography and socially mediated behavior.

Physiological limitations in diving ability limit the maximum depth and duration of a dive. Short-finned pilot whales show considerable sexual dimorphism (Olsen 2009), with adult females typically ranging between 3-4 m in length (Hohn et al. 2006) and adult males between 3.9-5.2 m in length (Kasuya and Marsh 1984). State 4 dives are longer and deeper than other dives and perhaps represent foraging behavior near the limit of the diving ability of this species off Cape Hatteras. Mori (2002) suggested that individuals of different body sizes might occupy different depths when feeding on patchy prey. However, we do not have complete sex or age class information for all of the individuals we sampled, so it is not possible to fully address this question. In addition, only one of the six tags with a duration greater than 6 hours was deployed on a female whale. However, this female, despite over 8 hours of tagging data, and with 34 dives, never made any State 2 or State 4 dives, and her deepest dive was to 362m (Table 4.1, Figure 4.4). Greater body size affords an increase in oxygen stores, allowing larger animals to dive for longer durations and to deeper depths where they may consume larger prey items to maximize net energy gain (Carbone et al. 2007). This is similar to the strategy seen during the daytime dives of short-finned pilot whales in Tenerife, in which individuals demonstrated a high-risk, high-gain strategy to target large, fast moving prey (Soto et al. 2008). The maximum depths and dive durations seen in Tenerife are very similar to those in our State 2 and State 4 dives, but the number of buzzes is strikingly different. The mean number of buzzes for State 2 off Cape Hatteras was 11.65 and for State 4 was 30.45, compared to 1.5 for the Tenerife animals (Soto et al. 2008). The number of buzzes we observed suggests that pilot whales off Cape Hatteras are foraging on multiple (perhaps small) prey items during the State 2 and 4 dives, unlike the foraging behavior shown off Tenerife (Soto et al. 2008).

Optimal diving theory predicts that individuals should maximize foraging subject to the constraints of oxygen stores (Houston and Carbone 1992). In State 4 dives, large-bodied pilot whales maximised the duration of time searching for prey, increased the number of prey encounters with prolonged bottom time, and increased their overall dive duration. However, it is clear that short-finned pilot whales off Cape Hatteras employ a variety of diving strategies, suggesting that physiological limits may not always drive diving behavior. Short-finned pilot whales off Cape Hatteras are known to exploit a wide range of food types with a predominance of pelagic, deep water squid species (Mintzer et al. 2008). Their diving ability enables them to exploit epipelagic, mesopelagic, and benthic habitats, suggesting that prey selection and availability could be driving the variation we see in diving behavior. There is no single solution

to the problem of exploiting mobile aquatic prey, and individual whales may vary their strategy dive by dive (Boyd 1997). We have no measure of success during prey capture attempts, but the variation in number of buzzes could reflect multiple failed foraging attempts or selection of different calorific prey items. For example, shorter State 2 and 3 dives could indicate animals breaking off from dives as a result of poor foraging success. In this case, we would predict that animals would switch states to target a more profitable prey layer. However, the probability of state persistence for all states is considerably higher than state transitions. Individual foraging specializations have been observed in a number of marine mammals including bottlenose dolphins (Smolker et al. 1997), Antarctic fur seals (Staniland et al. 2004), grey seals (Austin et al. 2004), narwhals (Laidre et al. 2003), and sea otters (Tinker et al. 2007). Individual pilot whales may also show preferences for specific prey types, foraging success or foraging specializations, that could contribute to the variation we observed in diving behavior. However, without observations of actual prey density, availability and consumption it is impossible to determine if individual specialization is a key driver of the observed differences.

The variation we observed in diving behavior could also be explained, in part, by the topography of the area. The slope area off Cape Hatteras has steep bathymetric gradients (Savidge and Bane 2001) and all DTAGs were deployed on animals within this area. We do not have fine-scale positional data for all of the tagged animals, but the differences in foraging depth we observed could be driven by bottom topography. Other studies of pilot whale diving behavior have shown animals foraging on or near the sea floor (Nawojchik et al. 2003) and this could explain some of the state allocations across individual whales. Pilot whales do not forage exclusively on benthic prey and their dive shapes do not consistently follow patterns seen by diving animals that feed in this manner (e.g. Grémillet et al. 1999).

Some of the observed variation in dive behavior is likely explained by social factors. Pilot whales are highly social animals which live in long-term, stable groups (Amos et al. 1993) and perform highly synchronous behavior (Senigaglia and Whitehead 2012). Social foraging and the linkages between individual and emergent group-level time budgets has been studied in a range of species (see Marshall et al. 2012), including long-finned pilot whales, in which whales from the same social group coordinate their foraging behavior (Visser et al. 2014). In this social foraging strategy, group members synchronize diving bouts, but do not synchronize each individual dive. This may aid in maintaining social group cohesion, especially in areas where large numbers of individual animals are present, such as our study site, where dense aggregations of pilot whales occur along the shelf break off Cape Hatteras (Best et al. 2012). The need for social cohesion may, therefore, dictate individual diving behavior, with animals making group-based foraging decisions (Conradt and Roper 2003). Our focal observations showed that individuals within a single social group show temporal synchrony of behaviors and often dive collectively, but we do not have simultaneous tagging data from multiple individuals in a group to determine if they all dive to similar depths. There may also be constraints imposed by the need of females to care for dependent calves with limited diving abilities. Sperm whale groups have been shown to alter dive behavior when a calf is present, with an adult more frequently observed at the surface compared to sperm whale groups without calves (Whitehead 1996).

The higher probability of state persistence than state transitions suggests that each state is indicative of a bout of behavior (see Chapter 3). We observed transitions between all states,

indicating that individuals do switch between different states. A recent study of sperm whale foraging behavior demonstrated how these whales switch between different prey layers in successive foraging dives based on acoustic information obtained during searching (Fais et al. 2015). It is possible that pilot whales conduct similar assessment of prey layers and use prior information to inform their foraging decisions, but it is also possible that transitions between states are driven by socially mediated or physiological factors.

In our analysis we incorporated only three observed variables as predictors of foraging behavior. Our model is, therefore, restricted to foraging-based predictors, making it difficult to tease apart other potential behaviors. Kinematic measures such as overall dynamic body acceleration (Qasem et al. 2012), or variation in heading, could be included in the model. However, because sub-surface behavior includes non-foraging activity, by adding these parameters we would be including unknown relationships between kinematic variables and non-foraging behavior, thereby increasing uncertainty and limiting further the explanation of the patterns we observed. A sensible extension would be to take the dives that we have high confidence are indicative of foraging (States 2 and 4) and explore differences between these states. Our model assumed no heterogeneity in individual diving behavior, based on the assumption that short-finned pilot whales employ a common foraging strategy across all individuals, *i.e.* we expect that all individuals are able to dive deeply. The fact that our states are distributed across multiple individuals suggests that diving states are broadly common across individuals, but it is clear that multiple factors contribute to differences in states, including physiological limitations, geographic topography, prey selection and abundance, and socially mediated behavior.

In conclusion, our analysis shows that diving behavior in this species is much more complex than a simple dichotomy of deep and shallow diving states. The variation we observed in diving behavior may be driven by a number of factors including individual specialization, foraging success, prey selection, topography, physiological limitation and socially mediated behavior. Individual short-finned pilot whales are able to adapt their diving strategy on a dive by dive basis, switch effectively between different diving states, while maintaining foraging efficiency and social cohesion.

Chapter 5: Conclusions and Implications for Future Research/Implementation

5.1 Is the Response of Odontocetes to Potential Threats Mediated by Patterns of Social Organization?

The work we describe here builds on the hypothesis that the responses displayed by certain odontocetes to MFAS, including avoidance and changes in vocal activity, represents a form of anti-predator behavior. As noted earlier in this report, Zimmer and Tyack (2007) were the first to suggest that the unusual stranding events of some beaked whales following exposure to MFAS might represent an extreme anti-predator response:

“One could therefore conclude that beaked whales may have a stereotyped avoidance reaction for predators with an antipredator benefit that outweighs any adverse effects if limited in time and intensity.”

They went on to note that:

“Testing the prediction of how beaked whales may respond to playback of killer whale calls and sonar will require measuring the surfacing and dive profile on exposure to the various sound stimuli and comparing that response to extensive baseline behavior.”

Our work has generated a significant amount of information on baseline behavior of odontocetes and addressed the response of two species to the calls of mammal-eating killer whales. Researchers have since picked up this thread and applied it to other species (e.g. Tyack et al. 2011). For example, Curé et al. (2015) recently demonstrated that humpback whales (*Megaptera novaeangliae*) responded strongly to the sound of a distant killer whale by stopping feeding and moving directly away from the sound source. The same research group conducted similar playback experiments with solitary male sperm whales and found that these animals responded by ceasing foraging, reducing vocal activity, and somewhat surprisingly, by clustering together (Curé et al. 2013).

The present research supported by SERDP has contributed to this body of work investigating key contextual factors of sound exposure and behavioral response in marine mammals. We have demonstrated that short-finned pilot whales and Risso’s dolphins react to the sound of mammal-eating killer whales in a manner that is consistent with our knowledge of their social organization. Pilot whales increased patterns of social cohesion, increased their vocal activity, and oriented towards the sound source. In contrast, Risso’s dolphins did not change their vocal activity and moved strongly away from the source.

Obviously, there is still considerable work to be done before we can establish linkages between the anti-predator response observed in these species and the range of potential responses to

tactical sonars (see below). Nevertheless, if these animals perceive MFAS and the sounds of predators in a similar manner, or even if they merely respond to the two sound types in the same way, we can infer much about the nature and likely magnitude of the potential risks of MFAS by understanding the anti-predator response of each species. Building on the results obtained in this project, future directed studies could directly inform and simplify the Navy's requests for authorizations to conduct training exercises by focusing attention on species, like beaked whales, that seem to exhibit potentially adverse responses under certain conditions. This work should include exposure to simulated MFAS signals as well as playbacks of the calls of mammal-eating killer whales (e.g. Tyack et al. 2011; DeRuiter et al. 2013).

Frid and Dill (2002) discuss some of the issues associated with this hypothesis in a broader evolutionary context. They noted that many prey species have evolved anti-predator responses to generalized threat stimuli and that these responses are typically invoked whenever a stimulus that shares common features of this class of perceived threat passes a particular threshold. They listed a series of interacting factors that may influence the risk of predation, including:

1. The structure of the environment;
2. Social factors;
3. The distribution and abundance of predators; and
4. The behavior of the predators themselves.

The last two factors are important, but are not necessarily directly relevant to the link between sociality and anti-predator response, so we do not consider them in detail here. Nevertheless, it is useful to consider briefly how the response of odontocetes might vary with changes in frequency of exposure to the calls of mammal-eating killer whales and how the nature of the signal itself may convey important information about both the presence and aspects of behavior of the predator. This seems particularly relevant given our observations that both pilot whales and Risso's dolphins respond strongly to only a subset of calls from mammal-eating killer whales. Below we consider how the first two factors, habitat and social structure, may influence the anti-predator response of odontocetes. We add body size to the list of considerations presented by Frid and Dill (2002), given the general observation that small-bodied dolphins and porpoises are clearly more vulnerable to predation than, for instance, large-bodied sperm whales.

Odontocetes inhabit an enormous variety of habitats from coastal estuaries to the open ocean, presenting dolphins, porpoises and toothed whales with varying levels of exposure to potential predators as well as a variety of potential response options. Complex coastal habitats offer a variety of potential refuges from predators, either as places to hide or environments in which attack and capture are impractical due to depth or topography. In addition, small-bodied coastal odontocete species in the genera *Phocoena* and *Cephalorhynchus* have evolved an acoustic repertoire that is not detectable by killer whales, and thus contributes to their cryptic anti-predator strategy (Moriska and Connor 2007). These species tend to occur in small groups, which also helps individual animals to avoid detection by killer whales (Gygax 2002).

In contrast the pelagic ocean offers little in the form of a refuge except, of course, in the vertical dimension for deep-diving whales. In fact, the brief surface periods and unusual pattern of diving exhibited by many beaked whales have been suggested to serve as a general anti-predatory

strategy, by limiting time spent in a dangerous environment (Tyack et al. 2006), because most killer whale attacks occur near the surface. This idea is supported by the fact that most beaked whales do not produce echolocation clicks (or other vocal signals) until they have descended to depths at which they are unlikely to encounter predators (Johnson et al. 2004). In addition, Cuvier's beaked whales (*Ziphius cavirostris*) spend more time near the surface at night when they are less vulnerable to predation (Schorr et al. 2014). Thus, the anti-predator response of these species relies first on crypsis and, if detected, on flight. These animals live in small groups of uncertain relatedness, but there seems to be no benefit to a coordinated group defense against predators.

One alternative to using depth as a refuge in the pelagic environment is to engage in social behavior that reduces the risk of predation. This can be achieved through cooperative behavior that enhances the probability of detecting, avoiding and perhaps deterring a predator (Pitman et al. 2001). Pilot whales and sperm whales fall into this category, in which related females and their kin live in stable social groups for many years. As noted above, the results we observed in our playback experiments support the hypothesis that the evolution of these unusually strong social bonds are, at least in part, a response to the risk of predation for pilot whales. That is, part of their response strategy to perceived risk is a form of social defense.

An alternative strategy in the open ocean is to live in large groups that may either confuse a predator or dilute the likelihood of individual capture. Many small-bodied pelagic odontocetes live in large groups, which has long been presumed to function as an anti-predator strategy (Norris and Dohl 1980). Unfortunately, we know little about the social organization of these species. We do not know, for example, anything about the strength of social bonds or whether related individuals display long-term associations. Nor have there been any studies of the behavioral response to the presence of predators. In fact, as noted above, we intended to include common dolphins as an experimental subject in our research, but were unable to attach DTAGs to this species for sufficient periods to conduct playback experiments.

At least one lineage of pelagic odontocetes, including the two extant species in the genus *Kogia*, have evolved an unusual combination of anti-predator strategies. These small-bodied animals are found alone or in small groups in the open ocean, where they are vulnerable to predation by killer whales (Dunphy-Daly et al. 2008). They employ a cryptic strategy, including a vocal repertoire that consists solely of clicks above the hearing range of killer whales (Moriska and Connor 2007). They are deep-diving species, which provides a potential refuge from surface predation, but also engage in a unique anti-predator behavior in which they emit a reddish-brown intestinal fluid, which forms a cloud in the water that may either provide a refuge or confuse a potential predator (Scott and Cordaro 1987). Thus, this genus occupies a particularly interesting space in the multi-dimensional continuum of anti-predator response.

Several species of mid-sized odontocetes, such as bottlenose and Risso's dolphins, fall along the continuum between the highly social species that exhibit group defense and the small-bodied species that occur in large groups. Until we conducted our field experiments, almost nothing was known about the response of these species to the presence of predators. The Risso's dolphins we studied demonstrated a response to the sound of mammal-eating killer whales that involved movement away from the perceived threat and was consistent with our knowledge of their social structure, which is considerably more labile than that of our other study species.

We suggest that there is considerable merit in pursuing this line of reasoning, by constructing a formal conceptual model of the response of odontocetes to potential threats and using interacting factors such as habitat, social structure and body-size as predictors of response. We envision using a matrix of these predictive factors to predict the behavioral response to a threat, at least in a coarse manner. Unfortunately, our knowledge of many species of odontocetes is still too rudimentary to allow for a complete formulation of such a matrix. Nevertheless, such an approach would lead to directly testable hypotheses and contrasts with selected species from different combinations of social structure, group size, and body size that would lead to generalizable results. Future work should attempt to fill these knowledge gaps by increasing our understanding of the social structure, particularly for pelagic delphinids, and documenting the response of other species odontocetes to the sounds of mammal-eating killer whales.

5.2 Biological functions of the monophonic and biphonic killer whale calls relative to killer whale social behavior and predator-prey dynamics

Mammal-eating killer whales are less vocal than other ecotypes of the species, because the mammalian prey of these predators can detect their calls (Deecke et al. 2005). To prevent detection by potential prey, mammal-eating killer whales limit both the rate and amplitude of vocal communication (Barrett-Leonard et al. 1996). Nevertheless, the prey of these whales, such as harbor seals (*Phoca vitulina*), are able to discriminate between the calls of mammal-eating and resident killer whales that prey on salmon (Deecke et al. 2005).

Mammal-eating killer whales, like all forms of this species, have an extremely varied vocal repertoire, including tonal whistles, echolocation clicks and pulsed calls. Included in this repertoire are overlapping, independently modulated components, referred to as *biphonic calls* (Filatova et al. 2012). These calls contain two distinct fundamental frequencies, both of which can exhibit harmonics, but their modulations are not linked and thus act as two overlapping, coincident but unrelated calls. When two independent sources are responsible for production of the sounds, they are referred to as *two-voiced calls* (Zollinger et al. 2008). We do not understand the mechanism of production of these calls in killer whales, so we refer to them as biphonic calls (Filatova et al. 2012).

Biphonic calls have been described in all mammal-eating killer whale populations sampled to date (Tyson et al. 2007). Analysis of killer whale vocal behavior is complicated by the variety of calls produced and the difficulty in ascribing any particular call type to a specific behavioral state. Resident killer whales in the waters off Kamchatka produced biphonic calls more frequently when multiple pods were present, suggesting that these calls are used as cohesive signals to identify specific matriline (Filatova et al. 2009). Biphonic calls are produced at significantly higher source levels, relative to monophonic calls, so they are audible over longer ranges. This further supports the concept that biphonic calls are used as group identifiers in encounters of killer whale social groups (Filatova et al. 2009; Miller 2006).

Some calls produced by mammal-eating killer whales contain other distinctive features, in addition to biphonation, that have been described as *nonlinear dynamics*. These features include frequency jumps, deterministic chaos, and sub-harmonics (Fitch et al. 2002; Tyson et al. 2007).

Some of these nonlinear dynamics, such as deterministic chaos (calls with random or unpredictable elements), are commonly found in alarm calls and are known to elicit strong reactions in mammals (Fitch et al. 2002).

The combination of biphonic calls, indicating the presence of more than one group of mammal-eating killer whales, and the presence of other non-linear phenomena, with their resemblance to alarm calls, may help to explain the strong avoidance reactions that we documented in pilot whales and Risso's dolphins exposed to stimuli containing these nonlinear features. However, it is important to note that we understand little about the response of potential prey to specific call types of mammal-eating killer whales. With the exception of the careful experimental work of Deecke et al. (2005), few prior studies have controlled for call type in previous playback experiments. We suggest that future work should explicitly consider call type as an experimental factor in playback experiments to tease apart the importance of biphonation, other nonlinear dynamics and additional features of these calls. Such work is complicated, of course, by the fact that most mammal-eating killer whales are mostly silent when actively hunting prey (Barrett-Leonard et al. 1996).

5.3 Research Gaps Related to Acoustic Ecology

Our research provides insights into the baseline behavior of short-finned pilot whales off Cape Hatteras, NC and Risso's dolphins in the Southern California Bight, and to the response of both species to the calls of predators. As noted above, we observed strong and divergent reactions of the two species to some mammal-eating killer whale calls, including increased call rates in pilot whales, but no measurable change in call counts for Risso's dolphins. Despite these findings, the acoustic ecology of both species remain poorly studied, including some basic information, such as a complete description of, and inference into, the functional significance of call types within their vocal repertoires, and the potential behavioral and environmental drivers of variation in production rates of these calls.

Describing the vocal repertoire of any acoustically active species is a fundamental prerequisite to investigations of behavior. Broad definitions of cetacean vocal signals exist, including social sounds and echolocation clicks (Richardson et al. 1995), but the function of calls likely varies across species. Identifying the function of each call type requires detailed study of individual vocal behavior and the responses of conspecifics (Janik 2009). Defining call types is challenging, because any classification system must reflect the animal's own categorization. Furthermore, the manner in which animals distinguish call types and subtypes may not be obvious to human observers (Janik 2009). Previous studies of pilot whale and Risso's dolphin vocal repertoires have shown a great diversity of calls in both species (Sayigh et al. 2013, Neves 2012), with indication of both repeated (produced by the same individual) and shared (produced by multiple individuals) calls. Both studies generated broad categories of calls, which likely included a mixture of different kinds of signals. In addition, individual calls may play different communicative roles or serve more than one function, including mediating interactions between social groups.

Future studies addressing call production and the effects of anthropogenic sound on vocal behaviour would be served by more detailed baseline study of the functional aspects of

vocalizations in both these species. Of course, the collection of this information on free-ranging individuals at sea is challenging. In particular, it is often difficult to determine context and the identity of calling animals, but research methods using an appropriate scale of behavioral observations (Altmann 1974) and passive acoustic localization techniques (Quick et al. 2008) have provided insight into context specificity (see Janik 2009 for review). We recommend that future studies employ these methodologies to elucidate functional aspects of pilot whale and Risso's dolphin calls in greater detail and believe strongly that such work would dramatically increase our ability to understand behavioral responses to disturbance.

It is also important to understand the biological and environmental drivers that may produce variation in the call rates of pilot whales and Risso's dolphins. Previous studies with bottlenose dolphins (*Tursiops* sp.) have shown variation in call rates in different social contexts, including mother-calf separations (Smolker et al. 1993), agonistic interactions between male alliances (Watwood et al. 2005) and with behavioural state and group size (Quick and Janik 2008). For example, the sound production of Risso's dolphins in Gran Canaria, Spain, was affected by behaviour patterns, group size and water depth (Neves 2012). And short-finned pilot whales are known to decrease their production of social calls when at depth (Jensen et al. 2011). It would be helpful to document baseline patterns of vocal activity in both these species and to determine how these rates vary with a range of social, ecological and environmental factors. Such fundamental information would dramatically increase our ability to understand behavioral responses to a variety of factors.

Tyack (2009a) and Zimmer and Tyack (2007) noted the similarities between the acoustic signals used in tactical, mid-frequency military sonar (MFAS) and the social sounds made by mammal-eating killer whales. In the present study we showed that both short-finned pilot whales and Risso's dolphins responded strongly to calls containing non-linear phenomena, but not to pure tone calls of mammal-eating killer whales. This suggests that structural features of these signals play critical contextual roles in determining the probability of response to potential threats in odontocete cetaceans. Non-linear phenomena are common in nonhuman mammal vocal repertoires (Fitch et al. 2002), including killer whales (Tyson et al. 2007, Miller et al. 2007) and short-finned pilot whales (Sayigh et al. 2013), but the potential functions of these phenomena are still poorly understood. We recommend further study of calls that contain non-linear phenomena across a variety of species, to determine whether they are functionally related to predation or predator avoidance.

5.4 Similarities between killer whale signals and MFAS sound profiles

As noted earlier in this report, other researchers have noted general similarities with and frequency overlap between MFAS signals and those produced by marine mammal-eating killer whales (Zimmer and Tyack 2007; Tyack et al. 2011). This correspondence led to the hypothesis that the response of some odontocete cetaceans to MFAS was, in essence, a predator avoidance strategy. Our work is cast in this context and, together with the results of several related studies of the response of cetaceans to simulated and actual MFAS, allow us to identify specific opportunities for future research.

First, as noted above, social signals produced by mammal-eating killer whales occur in a variety of general and specific types. We observed stronger behavioral responses to killer whale signals containing several distinct structural components, including “biphonic” calls, as we refer to them above. These calls are distinguished by disharmonic, asynchronized elements, meaning they do not occur as harmonics of one another. Further, while some of these calls have particular frequency modulated segments, elements of many biphonic calls have relatively continuous frequency components, often with their own harmonic elements.

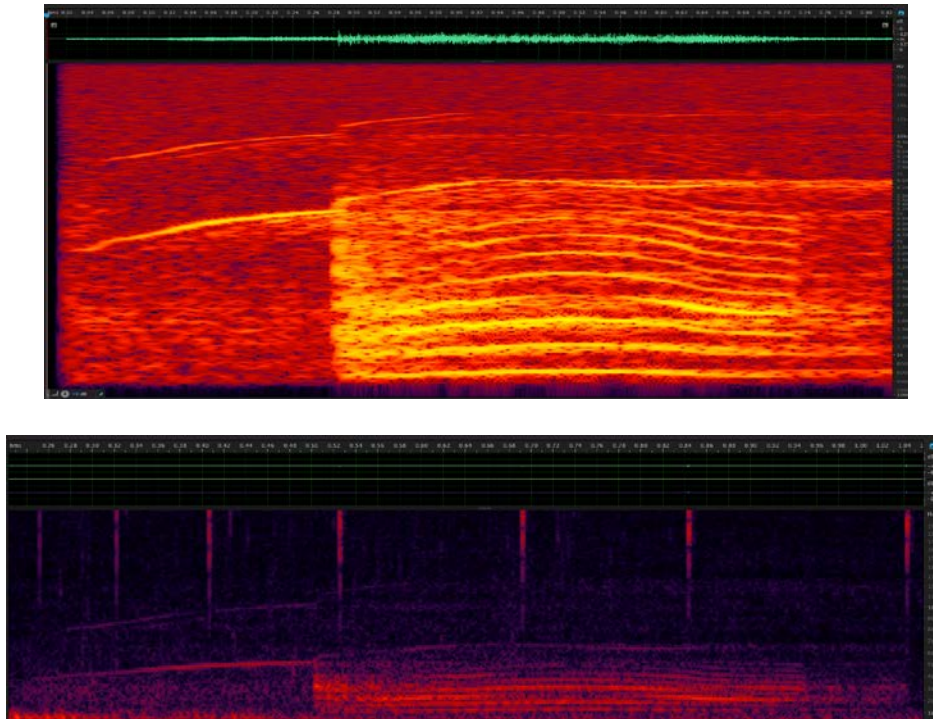


Figure 5.1. Spectrograms of biphonic calls from a mammal-eating killer whale from the LWBBUSS (top) and received on a DTAG on a short-finned pilot whale off Cape Hatteras (below).

This can be seen in the two signal spectrograms depicted above (Figure 5.1) showing a biphonic call from a mammal-eating killer whale, as it was projected from the LWBBUSS sound source (top) and as it was received from a tag deployed on a short-finned pilot whale off Cape Hatteras (bottom). Note the introductory upsweep in the signal followed by a harmonically rich segment in both the source and received signal, and the slightly extended reverberation of the signal in the signal on the tag recorded at a range of several hundred meters.

Below we compare this killer whale call with simulated and actual Navy MFAS used in the SOCAL-BRS study off southern California to illustrate some of the similar aspects of these signal types. The first sonar signal is a simulated MFAS signal waveform, recorded at the sound source (Figure 5.2A) and from a DTAG deployed on a blue whale (Figure 5.2B; from Southall et al. 2012). This sonar signal was generated to simulate an actual 53C MFAS signal with three distinct elements, consisting of a frequency upsweep and tonal elements, with a total duration of ~1.5s. In the signal recorded on the whale, the reverberation of signal energy is particularly evident.

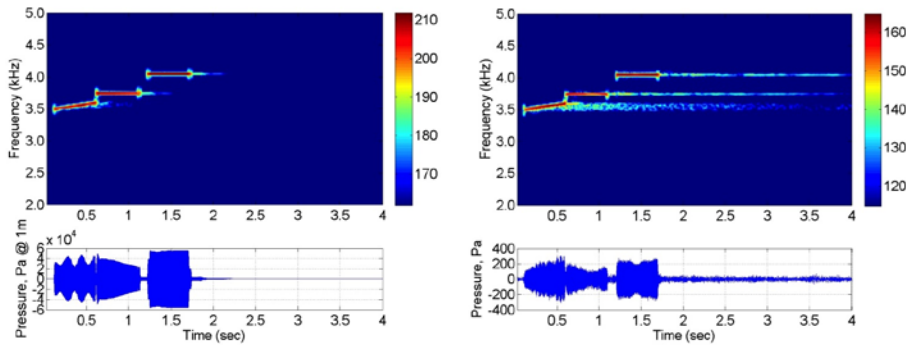


Figure 5.2. Simulated MFAS signal recorded at the source (A) and on a DTAG deployed on a blue whale off southern California (B).

Real MFAS signals also share some components with the biphonic calls of mammal-eating killer whales. In Figure 5.3 we present two examples of such signals recorded from DTAGs deployed on blue whales in the SOCAL-BRS project. The top figure shows a two-element MFAS signal from a 53C surface ship, where the source signal is also approximately 1.5s with a very distinct reverberation that lasts for ~20s. The lower figure shows an incidental exposure to two pings from a helicopter dipping sonar, with a somewhat similar general multi-note structure with reverberation at a slightly higher overall frequency.

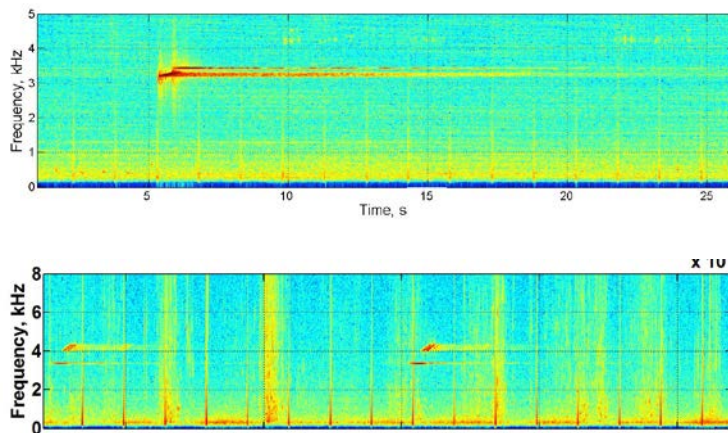


Figure 5.3. Two-element MFAS signal from a 53C surface vessel (top) and two pings from a helicopter dipping sonar (bottom), both recorded off southern California.

Clearly there are important similarities (and differences) amongst these signal types. The biphonic killer whale calls and MFAS signals are generally similar in frequency content and duration, with varying degrees of reverberation when received by animals, and both signal types include asynchronous tonal and frequency modulated elements. However, these similarities alone do not resolve the question of whether responses to MFAS are, indeed, some form of anti-predator response. Nevertheless, we found the strongest responses of pilot whales and Risso's dolphins to a subset of mammal-eating killer whale signals that share general structural features

with MFAS signals. The fact that we have induced strong responses experimentally in these species at relatively low Received Levels, rather than to more uniform frequency modulated calls that lack disharmonic tonal signals, is important and suggests that additional investigation is warranted. These results provide directly testable hypotheses that may have major implications for future Navy environmental impact assessments.

We suggest that future work should consider the relative importance of particular aspects of the biphonic calls of mammal-eating killer whales, such as biphonation and deterministic chaos, and MFAS signals in eliciting behavioral responses. This research should examine the potential importance of frequency modulation patterns and order relative to tonal elements and the extent to which reverberation may indicate a spatial context (e.g. distance to the source) in ways that mediate potential behavioral responses.

A straightforward approach to this problem would be to conduct playback experiments, similar to those described above, with MFAS signals and mammal-eating killer whale calls that have been digitally manipulated. The calls should be manipulated in a manner that would facilitate identification the specific feature(s) of the calls that elicit the strong responses we observed. For example, MFAS and calls of mammal-eating killer whales could be manipulated to remove certain frequency components or to manipulate the chaotic portion of the stimulus. In such work, careful consideration should be given to the exact type of signal manipulation to ensure that field experiments provide the greatest power possible to determine which specific aspects of these signals evokes a response in focal animals.

Literature Cited

- Alcock, J. 2005. Animal behavior: an evolutionary approach (8th ed.). Sunderland, MA: Sinauer Associates.
- Altman, R.M. 2007. Mixed hidden Markov models: an extension of the hidden Markov model to the longitudinal data setting. *J. Am. Stat. Assoc.* 102(477): 201–210.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49(3): 227–266.
- Alves, F., A. Dinis, C. Ribeiro, C. Nicolau, M. Kaufmann, C.M. Fortuna, et al. 2013a. Daytime dive characteristics from six short-finned pilot whales *Globicephala macrorhynchus* off Madeira Island. *Arquipelago. Life and Marine Sciences* 31: 1–8.
- Alves, F., S. Quéroutil, A. Dinis, C. Nicolau, C. Ribeiro, L. Freitas, et al. 2013b. Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 23(5): 758–776. <http://doi.org/10.1002/aqc.2332>
- Amos, B., C. Schlötterer, and D. Tautz. 1993. Social structure of pilot whales revealed by analytical DNA profiling. *Science* 260(5108): 670–672.
- Antunes, R., P.H. Kvadsheim, F.P.A Lam, P.L. Tyack, L. Thomas, P.J. Wensveen, et al. 2014. High thresholds for avoidance of sonar by free-ranging long-finned pilot whales (*Globicephala melas*). *Marine pollution bulletin* 83(1): 165–180.
- Austin, D., W.D. Bowen, and J.I. McMillan. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. *Oikos* 105: 15–30.
- Austin, D., W.D. Bowen, J.I. McMillan, and S.J. Iverson. 2006. Linking movement, diving, and habitat to foraging success in a large marine predator. *Ecology* 87(12): 3095–3108. [http://doi.org/10.1890/0012-9658\(2006\)87\[3095:LMDAHT\]2.0.CO;2](http://doi.org/10.1890/0012-9658(2006)87[3095:LMDAHT]2.0.CO;2)
- Baechler, J., C.A. Beck, and W.D. Bowen. 2002. Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology* 80(9): 1569–1577. <http://doi.org/10.1139/z02-150>
- Baird, R.W., J.F. Borsani, M.B. Hanson, and P.L. Tyack. 2002. Diving and night-time behaviour of long-finned pilot whales in the Ligurian Sea. *Marine Ecology Progress Series* 237: 301–305.

- Barrett-Lennard, L.G., J.K.B. Ford, and K.A. Heise. 1996. The mixed blessing of echolocation: Differences in sonar use by fish-eating and mammal-eating killer whales. *Animal Behaviour* 51: 553–565.
- Bart, J., M.A. Fligner, and W.I. Notz. 2009. *Sampling and Statistical Methods for Behavioral Ecologists*. Cambridge: Cambridge University Press.
<http://doi.org/10.1017/CBO9780511612572>
- Berens, P. 2009. CircStat: a MATLAB toolbox for circular statistics. *J Stat Softw.*
- Best, B.D., P.N. Halpin, A.J. Read, E. Fujioka, C.P. Good, E.A. LaBrecque, et al. 2012. Online cetacean habitat modeling system for the U.S. East Coast and Gulf of Mexico. *Endangered Species Research* 18: 1-15.
- Blesdoe, E. K. and D.T. Blumstein. 2014. What is the sound of fear? Behavioral responses of white-crowned sparrows *Zonotrichia leucophrys* to synthesized nonlinear acoustic phenomena. *Curr Zool* 60: 534-41.
- Bloch, D. and C. Lockyer. 1988. Killer whales (*Orcinus orca*) in Faroese waters.
- Blumstein, D. T. and C. Récapet. 2009. The Sound of Arousal: The Addition of Novel Non-linearities Increases Responsiveness in Marmot Alarm Calls. *Ethology* 115(11): 1074–1081.
<http://doi.org/10.1111/j.1439-0310.2009.01691.x>
- Boeuf, B.J.L., D.P. Costa, A.C. Huntley, and S.D. Feldkamp. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Canadian Journal of Zoology* 66(2): 446–458. <http://doi.org/10.1139/z88-064>
- Bowen, W.D., D. Tully and D.J. Boness. 2002. Prey-dependent foraging tactics and prey profitability in a marine mammal. *Marine Ecology Progress Series* 244: 235-245.
- Boyd, I. L. 1997. The behavioural and physiological ecology of diving. *Trends in Ecology and Evolution* 12: 213–217.
- Carbone, C., A. Teacher, and J.M. Rowcliffe. 2007. The costs of carnivory. *PLoS Biol* 5(2): e22.
<http://dio.org/10.1371/journal.pbio.0050022>.
- Caro, T. 2005. *Antipredator Defenses in Birds and Mammals*. University of Chicago Press.
- Connor, R.C. 2000. Group living in whales and dolphins. *Cetacean Societies: Field Studies of Dolphins and Whales*. 199-218.
- Conradt, L. and T.J. Roper. 2003. Group decision-making in animals. *Nature* 421: 155-158.
- Costa, D.P. and N.J. Gales. 2000. Foraging energetics and diving behavior of lactating New Zealand sea lions, *Phocarcos hookeri*. *Journal of Experimental Biology* 20(23): 3655-3665.

- Costa, D.P., C.E. Kuhn, M.J. Weise, S.A. Shaffer, and J.P.Y. Arnould. 2004. When does physiology limit the foraging behaviour of freely diving mammals? International Congress Series. 1275: 359–366. <http://doi.org/10.1016/j.ics.2004.08.058>
- Cox, T.M., T.J. Ragen, A.J. Read, and E. Vos. 2006. Understanding the impacts of anthropogenic sound on beaked whales. *Journal of Cetacean Research and Management* 7: 177-187.
- Crain, D.D., A.S. Friedlaender, D.W. Johnston, D.P. Nowacek, B.L. Roberts, K.W. Urian, et al. 2014. A quantitative analysis of the response of short-finned pilot whales, *Globicephala macrorhynchus*, to biopsy sampling. *Marine Mammal Science* 30: 819-826.
- Curé, C., R. Antunes, F. Samarra, A.C. Alves, F. Visser, P.H. Kvadsheim, et al. 2012. Pilot whales attracted to killer whale sounds: Acoustically-mediated interspecific interactions in cetaceans. *PLoS One* 7:e52201
- Curé, C., R. Antunes, A.C. Alves, and F. Visser. 2013. Responses of male sperm whales (*Physeter macrocephalus*) to killer whale sounds; implications for anti-predator strategies. *Scientific Reports* 3: 1579. <http://doi.org/10.1038/srep1579>
- Curé, C., L.D. Sivle, F. Visser, and P.J. Wensveen. 2015. Predator sound playbacks reveal strong avoidance responses in a fight strategist baleen whale. *Marine Ecology Progress Series* 526: 267-282.
- Curio, E., U. Ernst, and W. Vieth. 1978. The adaptive significance of avian mobbing. *Zeitschrift Für Tierpsychologie* 48(2): 184-202.
- D'Amico, A., R.C. Gisiner, D.R. Ketten, J.A. Hammock, C. Johnson, P.L. Tyack, et al. 2009. Beaked whale strandings and naval exercises. *Aquatic Mammals* 35: 452-472.
- de Stephanis, R., P. Verborgh, S. Pérez, R. Esteban, L. Minvielle-Sebastia, and C. Guinet. 2008. Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Acta Ethologica* 11(2): 81–94. <http://doi.org/10.1007/s10211-008-0045-2>
- Deecke, V.B. 2006. Studying marine mammal cognition in the wild: A review of four decades of playback experiments. *Aquatic Mammals* 32: 461-482.
- Deecke, V.B., P. Slater, and J. Ford. 2002. Selective habituation shapes acoustic predator recognition in harbour seals. *Nature* 420: 171–173.
- Deecke, V.B., J. Ford, and P. Slater. 2005. The vocal behaviour of mammal-eating killer whales: communicating with costly calls. *Animal Behaviour*. 69(2): 395-405.
- DeRuiter, S.L., B.L. Southall, J. Calambokidis, W.M.X. Zimmer, D. Sadykova, E.A. Falcone, et al. 2013. First direct measurements of behavioral responses by Cuvier's beaked whales to

- mid-frequency active sonar. *Proceedings of the Royal Society of London, Biology Letters* 9: 20130223–20130223. <http://doi.org/10.1098/rspb.2011.2088>.
- Donovan, G. P., and T. Gunnlaugsson. 1989. North Atlantic Sightings Survey 1987: report of the aerial survey off Iceland. *Rep Int Whal Commn.* 39: 437-41.
- Dunn, C. and D. Claridge. 2013. Killer whale (*Orcinus orca*) occurrence and predation in the Bahamas. *Journal of the Marine Biological Association of the United Kingdom.* 94(06): 1305-1309. <http://doi.org/10.1017/S0025315413000908>.
- Dunphy-Daly, M.M., M.R. Heithaus, and D.E. Claridge. 2008. Temporal variation in dwarf sperm whale (*Kogia sima*) habitat use and group size off Great Abaco Island, Bahamas. *Marine Mammal Science* 24: 171–182.
- Fahlman, A., P.L. Tyack, P.J.O. Miller, and P.H. Kvadsheim. 2014. How man-made interference might cause gas bubble emboli in deep diving whales. *Frontiers in Physiology* 5: 13. <http://doi.org/10.3389/fphys.2014.00013>
- Fais, A., N.A. Soto, M. Johnson, C. Pérez-González, P.J.O. Miller, and P.T. Madsen. 2015. Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. *Behavioral Ecology and Sociobiology* 69: 663-674.
- Fernández, A., J.F. Edwards, F. Rodriguez, A.E. de los Monteros, P. Herraiz, P. Castro, et al. 2005. “Gas and Fat Embolic Syndrome” Involving a Mass Stranding of Beaked Whales (Family Ziphiidae) Exposed to Anthropogenic Sonar Signals. *Veterinary Pathology* 42(4): 446–457. <http://doi.org/10.1354/vp.42-4-446>
- Filatova, O.A., I.D. Fedutin, M.M. Nagaylik, A.M. Burdin, and E. Hoyt. 2009. Usage of monophonic and biphonic calls by free-ranging resident killer whales (*Orcinus orca*) in Kamchatka, Russian Far East. *Acta Ethologica* 12: 37-44.
- Filatova, O.A., V. B. Deecke, J.K.B. Ford, C.O. Matkin, L.G. Barrett-Leonard, M.A. Guzeev, et al. 2012. Call diversity in the North Pacific killer whale populations: implications for dialect evolution and population history. *Animal Behaviour* 83: 595–603.
- Fish, F.E. 2006. The myth and reality of Gray's paradox: implication of dolphin drag reduction for technology. *Bioinspiration & Biomimetics* 1(2): R17–25. <http://doi.org/10.1088/1748-3182/1/2/R01>
- Fitch, W.T., J. Neubauer, and H. Herzl. 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour* 63: 407-418.
- Ford, J.K.B. and R.R. Reeves. 2008. Fight or flight: antipredator strategies of baleen whales. *Mammal Review* 38(1): 50–86. <http://doi.org/10.1111/j.1365-2907.2008.00118.x>
- Forney, G.D. 1973. The Viterbi algorithm. *Proc. IEEE* 61: 268-278.

- Frid, A. and L. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology* 6: 11-27.
- Gallon, S., F. Bailleul, J.B. Charrassin, C. Guinet, C.A. Bost, Y. Handrich, and M. Hindell. 2013. Identifying foraging events in deep diving southern elephant seals, *Mirounga leonina*, using acceleration data loggers. *Deep Sea Research Part II: Topical Studies in Oceanography* 88-89: 14–22. <http://doi.org/10.1016/j.dsr2.2012.09.002>
- Gaspari, S. 2004. Social and population structure of striped and Risso's dolphins in the Mediterranean Sea. Ph.D. Thesis, University of Durham, Durham, U.K.
- Goldbogen, J. A., B.L. Southall, S.L. DeRuiter, J. Calambokidis, A.S. Friedlaender, E.L. Hazen, et al. 2013. Blue whales respond to simulated mid-frequency military sonar. *Proceedings. Biological Sciences / the Royal Society* 280(1765): 20130657–20130657. <http://doi.org/10.1098/rspb.2013.0657>
- Grémillet, D., R.P. Wilson, S. Storch, and Y. Gary. 1999. Three-dimensional space utilization by a marine predator. *Marine Ecology Progress Series* 183: 263-273.
- Gygax, L. 2002. Evolution of group size in the dolphins and porpoises: interspecific consistency of intraspecific patterns. *Behavioral Ecology* 13: 583–590.
- Hairr, J. 2012. Killer whales (*Orcinus orca*) off the North Carolina coast 1709-2011. *Journal of the North Carolina Academy of Sciences* 128: 39-43.
- Harris, C.M., L. Thomas, D. Sadykova, S.L. DeRuiter, P.L. Tyack, B.L. Southall, et al. 2016. The challenges of analyzing behavioral response study data: An overview of the MOCHA (Multi-study ocean acoustics human effects analysis) project. In: *Effects of Noise on Aquatic Life II. Advances in Experimental Medicine and Biology* 875: 399-407.
- Hartman, K.L., F. Visser, and A.J.E. Hendricks. 2008. Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: a stratified community based on highly associated social units. *Canadian Journal of Zoology* 86: 294-306.
- Hazen, E.L., A.S. Friedlaender, and J.A. Goldbogen. 2015. Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Science Advances* 1(9): e1500469–e1500469. <http://doi.org/10.1126/sciadv.1500469>
- Heide-Jørgensen M.P., D. Bloch, E. Stefansson, B. Mikkelsen, L.H. Ofstad, and R. Dietz. 2002. Diving behaviour of long-finned pilot whales *Globicephala melas* around the Faroe Islands. *Wildlife Biology* 8: 307–13.
- Heimlich-Boran, J.R. 1993. Social Organisation of the Short-finned Pilot Whale, *Globicephala macrorhynchus*, with Special Reference to the Comparative Social Ecology of Delphinids.

- Hohn, A.A., D.S. Rotstien, C.A. Harms, and B.L. Southall. 2006. Report on Marine Mammal Unusual Mortality Event UMESE0501Sp: Multispecies Mass Stranding of Pilot Whales (*Globicephala macrorhynchus*), Minke Whale (*Balaenoptera acutorostrata*), and Dwarf Sperm Whales (*Kogia sima*) in North Carolina on 15-16 January 2005. NOAA Technical Memorandum NMFS-SEFSC-537. 222pp.
- Højsgaard, S., U. Halekoh, and J. Yan. 2006. Geepack: The R package geepack for Generalized Estimating Equations 15(2): 1–11.
- Hooker, S.K. and R.W. Baird. 2001. Diving and ranging behaviour of odontocetes: a methodological review and critique. Mammal Review 31: 81-105.
- Hooker, S.K., R.W. Baird, and A. Fahlman. 2009. Could beaked whales get the bends? Effect of diving behaviour and physiology on modelled gas exchange for three species: *Ziphius cavirostris*, *Mesoplodon densirostris* and *Hyperoodon ampullatus*. Respiratory Physiology & Neurobiology 167(3): 235–246.
- Hooker, S.K., A. Fahlman, M.J. Moore, N.A. Soto, Y. Bernaldo de Quiros, A.O. Brubakk, et al. 2012. Deadly diving? Physiological and behavioural management of decompression stress in diving mammals. Proceedings of the Royal Society B: Biological Sciences 279(1731): 1041–1050.
- Hothorn, T. and A. Zeileis. 2014. partykit: A Modular Toolkit for Recursive Partytioning in R. Working Papers in Economics and Statistics, Research Platform Empirical and Experimental Economics. Retrieved from <http://EconPapers.RePEc.org/RePEc:inn:wpaper:2014-10>
- Hothorn, T., K. Hornik and A. Zeileis. 2012. Unbiased Recursive Partitioning: A Conditional Inference Framework. Journal of Computational and Graphical Statistics 15(3): 651–674. <http://doi.org/10.1198/106186006X133933>
- Houston, A.I. and C. Carbone. 1992. The optimal allocation of time during the diving cycle. Behav. Ecol. 3: 255–265. <http://doi.org/10.1093/beheco/3.3.255>.
- Isbell, L.A. 1994. Predation on primates: ecological patterns and evolutionary consequences. Evolutionary Anthropology: Issues, News, and Reviews. 3(2): 61-71.
- Janik, V.M. 2009. Acoustic communication in Delphinids. Advances in the study of behavior 40: 123-157.
- Jefferson, T.A., P.J. Stacey, and R.W. Baird. 1991. A review of Killer Whale interactions with other marine mammals: predation to co-existence. Mammal Review 21(4): 151–180. <http://doi.org/10.1111/j.1365-2907.1991.tb00291.x>

- Jensen, F.H., J.M. Perez, M. Johnson, N. Aguilar de Soto, and P.T. Madsen. 2011. Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. *Proceedings of the Royal Society B* 278: 017–3025.
- Johnson, M.P. and P.L. Tyack. 2003. A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *Oceanic Engineering, IEEE Journal of Oceanic Engineering* 28: 3–12.
- Johnson, M., P.T. Madsen, W.M.X. Zimmer, N.A. Soto, and P.L. Tyack. 2004. Beaked whales echolocate on prey. *Proceedings of the Royal Society of London, Biology Letters* 271: S383–386.
- Johnson, M., N.A. Soto and P.T. Madsen. 2009. Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review. *Marine Ecology Progress Series* 395: 55–73.
- Karniski, C., E.M. Patterson, E. Krzyszczyk, and J. Mann. 2015. Determining cetacean activity budgets: a comparison of surveys and individual focal follows. *Marine Mammal Science* 31: 839–852.
- Kasuya, T. and H. Marsh. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. In: *Reproduction in Whales, Dolphins and Porpoises*. W.F. Perrin, R.L. Brownell Jr. and D.P. DeMaster (eds). IWC Reports, Special Issue 6: 259–310.
- Laidre, K.L., M.P. Heide- Jørgensen, R. Dietz, R.C. Hobbs, and O.A. Jørgensen. 2003. Deep-diving by narwhals *Monodon monoceros*: differences in foraging behaviour between wintering areas? *Marine Ecology Progress Series* 261: 269–281.
- Langrock, R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J.M. Morales. 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions *Ecology* 93: 2336–2342.
- LeDuc, R. 2009. Delphinids, Overview. In *Encyclopedia of Marine Mammals*. pp. 298–302. Elsevier. <http://doi.org/10.1016/B978-0-12-373553-9.00072-9>
- Lesage, V., M.O. Hammill, and K.M. Kovacs. 1999. Functional classification of harbor seal (*Phoca vitulina*) dives using depth profiles, swimming velocity, and an index of foraging success. *Canadian Journal of Zoology* 77(1): 74–87.
- Liaw, A. and M. Wiener. 2002. Classification and regression by randomForest. *R News*. 2(3): 18–22.
- Luque, S.P. 2007. Diving behaviour analysis in R. *R News*. 7(3): 8–14.
- Luque, S.P. and C. Guinet. 2007. A maximum likelihood approach for identifying dive bouts

- improves accuracy, precision and objectivity. *Behaviour* 144(11): 1315–1332.
<http://doi.org/10.1163/156853907782418213>
- Madsen, P.T., M. Wahlberg, J. Tougaard, and K. Lucke. 2006. Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs.
- Mahaffy, S.D., R.W. Baird, D.J. McSweeney, D.L. Webster, and G.S. Schorr. 2015. High site fidelity, strong associations, and long-term bonds: Short-finned pilot whales off the island of Hawai‘i. *Marine Mammal Science* 31(4): 1427–1451. <http://doi.org/10.1111/mms.12234>
- Marino, L. 2002. Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution* 59(1-2): 21-32.
- Marshall, H.H., A.J. Carter, J.M. Rowcliffe, and G. Cowlshaw. 2012. Linking social foraging behaviour with individual time budgets and emergent group-level phenomena. *Animal Behavior* 84: 1295-1305.
- MATLAB. 2012. Version 8.0.0.783 (R2012b). Natick, Massachusetts: The Mathworks Inc.
- Maybaum, H.L. 1993. Responses of humpback whales to sonar sounds. *The Journal of the Acoustical Society of America* 94(3): 1848–1849. <http://doi.org/10.1121/1.407710>
- McGregor, P.K. 2000. Playback experiments: design and analysis. *Acta Ethologica* 3(1): 3–8.
<http://doi.org/10.1007/s102110000023>
- Milinski, M. 1984. A predator's costs of overcoming the confusion-effect of swarming prey. *Animal Behaviour* 32(4): 1157–1162. [http://doi.org/10.1016/S0003-3472\(84\)80232-8](http://doi.org/10.1016/S0003-3472(84)80232-8)
- Miller, P.J.O. 2006. Diversity in sound pressure levels and estimated active space of resident killer whale vocalizations. *Journal of Comparative Physiology A* 192: 449-459.
- Miller, P.J.O., M.P. Johnson, and P.L. Tyack. 2004. Sperm whale behaviour indicates the use of echolocation click buzzes ‘creaks’ in prey capture. *Proceedings of the Royal Society of London B*, 271: 2239–2247.
- Miller, P.J.O., F.I.P. Samarra, and A. Perthuisson. 2007. Caller sex and orientation influence spectra of two-voice’ stereotyped calls produced by free-ranging killer whales *Orcinus orca*. *Journal of the Acoustical Society of America* 121: 3932–3937.
- Miller, P.J.O., P.H. Kvadsheim, F.-P.A. Lam, P.J. Wensveen, R. Antunes, A.C. Alves, et al. 2012. The Severity of Behavioral Changes Observed During Experimental Exposures of Killer (*Orcinus orca*), Long-Finned Pilot (*Globicephala melas*), and Sperm (*Physeter macrocephalus*) Whales to Naval Sonar. *Aquatic Mammals* 38(4): 362–401.
<http://doi.org/10.1578/am.38.4.2012.362>
- Miller, P.J.O., R.N. Antunes, P.J. Wensveen, F.I.P. Samarra, A.C. Alves, P.L. Tyack, et al. 2014.

- Dose-response relationships for the onset of avoidance of sonar by free-ranging killer whales. *The Journal of the Acoustical Society of America* 135(2): 975–993. <http://doi.org/10.1121/1.4861346>
- Mintzer, V.J., D.P. Gannon, N.B. Barros, and A.J. Read. 2008. Stomach contents of mass-stranded shortfinned pilot whales (*Globicephala macrorhynchus*) from North Carolina. *Marine Mammal Science* 24: 290–302.
- Mori Y. 1998. Optimal choice of foraging depth in divers. *Journal of Zoology* 245(03): 279–283.
- Mori, Y. 2002. Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology* 15: 269–276.
- Mori, Y., K. Yoda, and K. Sato. 2001. Defining dive bouts using a sequential differences analysis. *Behaviour* 138(11): 1451–1466. <http://doi.org/10.1163/156853901317367690>
- Moriska, T. and R.C. Connor. 2007. Predation by killer whales (*Orcinus orca*) and the evolution of whistle loss and narrow-band high frequency clicks in odontocetes. *Journal of Evolutionary Biology* 20: 1439–1458.
- Murray, K.A. and D. Rosauer. 2011. Integrating species traits with extrinsic threats: closing the gap between predicting and preventing species declines. *Proceedings of the Royal Society of London B: Biological Sciences* 278(1711): 1515–1523.
- National Marine Fisheries Service. 2006. Final consolidated Atlantic highly migratory species fishery management plan. 5(1): 200–210. <http://doi.org/10.1080/19425120.2013.786002>
- Nawojchik, R., D.J. St. Aubin, and A. Johnson. 2003. Movements and dive behavior of two stranded, rehabilitated long-finned pilot whales (*Globicephala melas*) in the northwest Atlantic. *Marine Mammal Science* 19: 232–239.
- Neves, S. 2012. Acoustic Behaviour of Risso’s dolphins, *Grampus griseus*, in the Canary Islands, Spain. Unpublished Ph.D. Thesis, University of St Andrews, UK.
- Norris, K.S. and T.P. Dohl. 1980. The structure and function of cetacean schools. Chapter 5 in: *Cetacean Behavior: Mechanisms and Functions* (edited by L.M. Herman). John Wiley & Sons, New York. 463 pp.
- Nowacek, D.P., L.H. Thorne, D.W. Johnston, and P.L. Tyack. 2007. Responses of cetaceans to anthropogenic noise. *Mammal Review* 37(2): 81–115. <http://doi.org/10.1111/j.1365-2907.2007.00104.x>
- Olson, P.A. 2009. Pilot whale *Globicephala melas* and *G. muerorhynchus* pp. 847–52 in *Encyclopedia of Marine Mammals*, Perrin, W.F., Wursig, B., and Thewissen, J.G.M. (eds.), Academic Press; 2nd edition, ISBN 0-12-551340-2.

- Oremus, M. 2008. Genetic and demographic investigation of population structure and social system in four delphinid species. (P.C.S. Baker, Ed.). ResearchSpace@Auckland.
- Parsons, E.C.M., S.J. Dolman, A.J. Wright, N.A. Rose, and W.C.G. Burns. 2008. Navy sonar and cetaceans: just how much does the gun need to smoke before we act? *Marine Pollution Bulletin* 56(7): 1248–1257. <http://doi.org/10.1016/j.marpolbul.2008.04.025>
- Pitman, R.L., L.T. Balance, S.L. Mesnick, and S.J. Chivers. 2001. Killer whale predation on sperm whales: observations and implications. *Marine Mammal Science* 17: 494-507.
- Qasem L., A. Cardew, A. Wilson, I. Griffiths, L.G. Halsey, E.L.C. Shepard, et al. 2012. Tri-Axial Dynamic Acceleration as a Proxy for Animal Energy Expenditure; Should We Be Summing Values or Calculating the Vector? *PLoS ONE* 7: e31187. <http://doi.org/10.1371/journal.pone.0031187>
- Quick, N.J. and V.M. Janik. 2008. Whistle rates of wild bottlenose dolphins: influences of group size and behavior. *Journal of Comparative Psychology* 122: 305-311.
- Quick N.J., L.R. Rendell, and V.M. Janik. 2008. A mobile acoustic localisation system for the study of free-ranging dolphins during focal follows. *Marine Mammal Science* 24: 979-989.
- R Core Development Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabiner, L.R. 1989. A Tutorial on Hidden Markov Models and selected applications in speech recognition. *Proceedings of the IEEE* 77: 257-285.
- Richardson W.J., C.R.J. Greene, C.I. Malme, and D.H. Thomson. 1995. *Marine Mammals and Noise*. San Diego CA: Academic Press Inc. 576 p.
- Robert-Coudert, Y. and M. Beaulieu. 2009. Diving into the world of biologging. *Endangered Species Research* 10: 21-27.
- Rosen, D.A.S., A.J. Winship, and L.A. Hoopes. 2007. Thermal and digestive constraints to foraging behaviour in marine mammals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 362(1487): 2151–2168. <http://doi.org/10.1098/rstb.2007.2108>
- Rubenstein, D.I. 1978. On Predation, competition, and the advantages of group living. In *Social Behavior*. pp. 205–231. Springer US. http://doi.org/10.1007/978-1-4684-2901-5_9
- Savidge, D.K. 2004. Gulf stream meander propagation past Cape Hatteras. *Journal of Physical Oceanography* 34(9): 2073-2085. [http://doi.org/10.1175/1520-0485\(2004\)034<2073:GSMPPC>2.0.CO;2](http://doi.org/10.1175/1520-0485(2004)034<2073:GSMPPC>2.0.CO;2)

- Savidge, D.K. and J.M. Bane Jr. 2001. Wind and Gulf Stream influences on along-shelf transport and off-shelf export at Cape Hatteras, North Carolina. *Journal of Geophysical Research* 106(C6): 11505.
- Sayigh, L., N. Quick, G. Hastie and P. Tyack. 2013. Repeated call types in short-finned pilot whales, *Globicephala macrorhynchus*. *Marine Mammal Science* 29: 312-324.
- Schorr, G.S., E.A. Falcone, D.J. Moretti, and R.D. Andrews. 2014. First long-term behavioral records from Cuvier's Beaked Whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS One* 9: e92633.
- Scott, M.D. and J.G. Cordaro. 1987. Behavioral observations of the dwarf sperm whale. *Marine Mammal Science* 3: 353-354.
- Senigaglia, V. and H. Whitehead. 2012. Synchronous breathing by pilot whales. *Marine Mammal Science* 28: 213-219.
- Seyfarth, R.M., D.L. Cheney, and P. Marler. 1980. Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science* 210(4471): 801–803. <http://doi.org/10.1126/science.7433999>
- Sibly, R.M., H.M.R. Nott and D.J. Fletcher. 1990. Splitting behaviour into bouts. *Animal Behaviour* 39(1):63–69. [http://doi.org/10.1016/S0003-3472\(05\)80726-2](http://doi.org/10.1016/S0003-3472(05)80726-2)
- Simon, M., M. Johnson, P.L. Tyack, and P.T. Madsen. 2009. Behaviour and kinematics of continuous ram filtration in bowhead whales (*Balaena mysticetus*). *Proceedings of the Royal Society B: Biological Sciences* 276(1674): 3819–3828. <http://doi.org/10.1098/rspb.2009.1135>
- Sivle, L.D., P.H. Kvadsheim, A. Fahlman, F.P. Lam, P.L. Tyack, and P. Miller. 2012. Changes in dive behaviour during naval sonar exposure in killer whales, long-finned pilot whales, and sperm whales. *Frontiers in Physiology* 3.
- Smolker, R.A., J. Mann, and B.B. Smuts. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behavioural Ecology and Sociobiology* 33: 393-402.
- Smolker, R., A. Richards, R. Connor, J. Mann, and P. Berggren. 1997. Sponge carrying by dolphins (Delphinidae, *Tursiops* sp.): a foraging specialization involving tool use? *Ethology* 103: 454–465.
- Soto, N.A., M.P. Johnson, P.T. Madsen, F. Diaz, I. Dominguez, A. Brito, et al. 2008. Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands) *Journal of Animal Ecology* 77: 936-947.
- Southall B.L., I. Boyd, P.L. Tyack, and D. Wartzok. 2008. Deep-diving odontocetes behavioral-

- response study (BRS). *Bioacoustics* 17(1-3): 186–188.
<http://doi.org/10.1080/09524622.2008.9753811>
- Southall, B.L., D. Moretti, B. Abraham, J. Calambokidis, S. DeRuiter and P.L. Tyack. 2012. Marine mammal behavioral response studies in southern California: Advances in technology and experimental methods. *Marine Technology Society Journal* 46: 48–59.
- Spitz J., A.W. Trites, V. Becquet, A. Brind'Amour, Y. Cherel, R. Galois, et al. 2012. Cost of living dictates what whales, dolphins and porpoises eat: The importance of prey quality on predator foraging strategies. *PLoS ONE* 7: e50096.
<http://doi.org/10.1371/journal.pone.0050096>
- Staniland, I.J., K. Reid, and I.L. Boyd. 2004. Comparing individual and spatial influences on foraging behaviour in Antarctic fur seals *Arctocephalus gazella*. *Marine Ecology Progress Series* 275: 263–274.
- Stanford, C.B. 2002. Avoiding Predators: Expectations and Evidence in Primate Antipredator Behavior. *International Journal of Primatology* 23(4): 741–757.
<http://doi.org/10.1023/A:1015572814388>
- Stephens P.A., C. Carbone, I.L. Boyd, J.M. McNamara, K.C. Harding, and A.I. Houston. 2008. The scaling of diving time budgets: insights from an optimality approach. *American Naturalist* 171: 305.
- Stimpert, A.K., S. DeRuiter, D. Moretti, A.S. Friedlaender, G. Schorr, E. Falcone, et al. 2014. Acoustic and foraging behavior of a tagged Baird's beaked whale (*Berardius bairdii*) exposed to simulated sonar. *Scientific Reports* 4: 7031.
<http://doi.org/10.1038/srep07031>
- Tamura, N. 1989. Snake-directed mobbing by the Formosan squirrel *Callosciurus erythraeus taiwanensis*. *Behavioral Ecology and Sociobiology* 24(3): 175-180.
- Tinker, M. T., D.P. Costa, J.A. Estes, and N. Wieringa. 2007. Individual dietary specialization and dive behaviour in the California sea otter: Using archival time–depth data to detect alternative foraging strategies. *Deep Sea Research Part II*: 54: 330–342.
- Tyack, P.L. 2009a. Human generated sound and marine mammals. *Physics Today* 62: 39-44.
- Tyack, P.L. 2009b. Acoustic playback experiments to study behavioral responses of free-ranging marine animals to anthropogenic sound. *Marine Ecology Progress Series* 395: 187-200.
- Tyack, P.L., M.P. Johnson, N.A. Soto, A. Sturlesse, and P.T. Madsen. 2006. Extreme diving behavior of beaked whale species *Ziphius cavirostris* and *Mesoplodon densirostris*. *Journal of Experimental Biology* 209: 4238–4253.

- Tyack, P.L., W.M.X. Zimmer, D. Moretti, B.L. Southall, D.E. Claridge, J.W. Durban, et al. 2011. Beaked whales respond to simulated and actual navy sonar. PLoS One 6: e17009.
- Tyson, R.B., D.P. Nowacek, and P.J.O. Miller. 2007. Nonlinear phenomena in the vocalizations of North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus orca*). Journal of the Acoustical Society of America 122: 1365-1373.
- Visser, F. 2013. Ceteacean Social Behavioral Response to Sonar. Kelp Marine Research Hoorn (Netherlands).
- Visser, F. 2014. Moving in concert: Social and migratory behaviour of dolphins and whales in the North Atlantic Ocean. (J. Huisman & G. J. Pierce, Eds.).
- Visser, F., P.J.O. Miller, R.N. Antunes, M.G. Oudejans, M.L. Mackenzie, K. Aoki, et al. 2014. The social context of individual foraging behaviour in long-finned pilot whales (*Globicephala melas*). Behaviour 151: 1453-1477
- Viviant, M., P. Monestiez, and C. Guinet. 2014. Can We Predict Foraging Success in a Marine Predator from Dive Patterns Only? Validation with Prey Capture Attempt Data. PloS One 9(3): e88503. <http://doi.org/10.1371/journal.pone.0088503>
- Watwood, S.L., E.C.G. Owen, P.L. Tyack, and R.S. Wells. 2005. Signature whistle use by temporarily restrained and free-swimming bottlenose dolphins, *Tursiops truncatus*. Animal Behaviour 69: 1373-1386.
- Wells, R.S., E.M. Fougères, A.G. Cooper, R.O. Stevens, M. Brodsky, R. Lingenfelser, et al. 2013. Movements and dive patterns of short-finned pilot whales, *Globicephala macrorhynchus*, released from a mass stranding in the Florida Keys. Aquatic Mammals 39: 61-72.
- Whitehead H. 1996. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioural Ecology and Sociobiology 38: 237-244.
- Whitehead, H. 2008. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press. <http://doi.org/10.7208/chicago/9780226895246.001.0001>
- Williams, T.M. 2009. Swimming. pp. 1140–1147 in Encyclopedia of Marine Mammals. Perrin, W. F., Wursig, B., and Thewissen, J. G. M. (eds.), Academic Press; 2nd edition, ISBN 0-12-551340-2.
- Zimmer, W.M.X. and P.L. Tyack. 2007. Repetitive shallow dives pose decompression risk in deep-diving beaked whales. Marine Mammal Science 23: 888-925.
- Zucchini, W. and I.L. MacDonald. 2009. Hidden Markov models for time series: an introduction using R. London:Chapman & Hall.

Zollinger, S.A., T. Riede, and R.A. Suthers. 2008. Two-voice complexity from a single side of the syrinx in northern mockingbird (*Mimus polyglottos*) vocalizations. *Journal of Experimental Biology* 211: 1978-1991.

Zuberbühler, K., D. Jenny, and R. Bshary. 2009. The Predator Deterrence Function of Primate Alarm Calls. *Ethology* 105(6): 477–490. <http://doi.org/10.1046/j.1439-0310.1999.00396.x>

Appendices

A. Supporting Data:

We have not included copies of all data collected on the project due to the extraordinary size of the overall data set, which is several terabytes. The data are all archived on redundant, secure servers at Duke, and these archived copies are separated from the copies used on a daily basis for analyses, i.e., the archived copies are not routinely accessed keeping them more secure. If SERDP would like copies of all these data, we can arrange for copies to be made and shipped.

B. List of Scientific/Technical Publications

In Print:

Harris, C.M., L. Thomas, D. Sadykova, S.L. DeRuiter, P.L. Tyack, B.L. Southall, et al. 2016. The challenges of analyzing behavioral response study data: An overview of the MOCHA (Multi-study ocean acoustics human effects analysis) project. In: Effects of Noise on Aquatic Life II. Advances in Experimental Medicine and Biology 875: 399-407.

Presentations:

Bowers, M., S. DeRuiter, A. Friedlaender, D. Nowacek, N. Quick, B. Southall, A. Read. Short finned Pilot Whales and Risso's Dolphins Respond Strongly and Divergently to Biphonic calls of Mammal-Eating Killer whales. 21st Biennial Conference on Marine Mammals. December 2015.

Nowacek, D.P., M. Bowers, A. Cannon, M. Hindell, L.E. Howle, M.M. Murray, D. Rittschof, K.A. Shorter, and M. Moore. The next generation of multi-sensor acoustic tags: sensors, applications and attachments. 166th Meeting of the Acoustical Society of America in San Francisco, CA. December 2013.

Quick, N., D. Nowacek, and A. Read. Hidden Markov Models reveal complexity in the diving behavior of short-finned pilot whales. 21st Biennial Conference on Marine Mammals. December 2015.